THE ECOLOGICAL COMPLEX CONTROLLING ACTIVITIES AND DISTRIBUTION OF IXODES RICINUS

Being a Thesis submitted for the
Degree of D.Sc. of Edinburgh University

by

JOHN MACLEOD, B.Sc., Ph.D.

April, 1935.

The following thesis consists of five papers dealing with the relation of the tick, Ixodes ricinus, to its general environment. Three of the papers have already been published, two in "Parasitology" (1934 and 1935), and one in "The Journal of Animal Ecology," 1934; the fourth paper has been accepted for publication in "Parasitology," and the fifth, being a philosophical interpretation of the experimentally obtained results, is being offered at present for publication in the same journal.

[*Reprinted from the* Journal of Animal Ecology,
Vol. 3, *No.* 2, pp. 161–164, *November*, 1934.]
 PRINTED IN GREAT BRITAIN

THE PART PLAYED BY ALTERNATIVE HOSTS IN MAINTAINING THE TICK POPULATION OF HILL PASTURES

By JOHN MACLEOD, B.Sc., Ph.D.

(*From the Moredun Research Institute, Gilmerton, Edinburgh.*)

(*With one Figure in the Text.*)

I. Introduction.

Parasites in general have a fairly specific host relationship, in that their host range is limited to one species in extreme cases, or, more commonly, to two or more nearly related species. In the absence of the normal host or hosts, the parasite will not, or cannot, adapt itself to other hosts. It is recognised, however, that certain parasites are less highly specialised, in that this specificity is less marked, and they are able to support themselves with more or less success on secondary or alternative hosts.

The importance of the question of alternative hosts is obvious in the case of parasites of economic significance, since it is clear that the facility with which a parasite can be eradicated will vary inversely with its adaptability to hosts other than the normal one. A modification of the same problem is presented by the survival of trypanosomes in the natural reservoirs represented by wild game, which act as alternative hosts for the vectors which transmit these same trypanosomes to domestic animals. It is apparent that this aspect of the ecology of parasites is of very considerable importance, and deserves greater attention than that so far devoted to it.

The writer is unaware of any studies of a quantitative nature on the part played by alternative hosts in perpetuating parasitic species, although many lists have been given of the possible alternative hosts for different parasites.

In the following work, which forms part of a general investigation of the bionomics of *Ixodes ricinus* L., the common tick of Britain, a qualitative and quantitative analysis has been made of the part played by wild mammals and birds in supporting the tick population of hill pastures.

II. Hosts of *Ixodes ricinus*.

A study of the possible hosts of *Ixodes ricinus* was made, the detailed results of which have already been recorded (MacLeod, 1933). It appears, from the writer's findings and those of other workers, that one or more stages of the tick could survive on the following warm-blooded hosts: *Mammals*: horse, cattle, deer, hedgehog, dog, fox, cat, stoat, weasel, ferret, hare, rabbit, rat, squirrel; *Birds*: siskin, hoodie crow, jackdaw, golden plover, kestrel, merlin, sparrowhawk, barn owl and grouse.

The great scope of this host range is of interest. It is important, however, to determine the extent, if any, to which a tick population can be supported in the absence of the sheep host, for the mere fact that occasional ticks may feed on the above alternative hosts is no proof that they could be maintained in any numbers if they were entirely dependent on hosts other than the sheep.

III. The experiment.

In the following experiment an area of tick-infested pasture in the Ettrick valley was separated from the rest of the farm. The original sheep-supported population of ticks was reduced until the only ticks present were those which had succeeded in surviving on alternative hosts. The method used was as follows. A 10-acre plot of typical hill pasture was fenced off in May 1929. This was surrounded by a "neutral area," 45 yards broad, to prevent unfed ticks crawling in from the surrounding pasture. The outer fence consisted of game-proof wire netting of $1\frac{1}{2}$ in. mesh, so that only the smaller forms of mammalian life could obtain ingress. It is known, however, that hares succeeded in entering the area by leaping the boundaries. The original tick population was eradicated in the following manner. A dipping tank was constructed in one corner of the enclosed area. Twenty-one sheep were dipped to free them from attached ticks, and liberated on the central area. They were dipped every fifth day for several weeks, and then removed. In the autumn of the same year, forty-two sheep were grazed on the area and dipped every third day for six successive dippings. This procedure was again repeated in the autumn of 1930, twenty-six sheep being dipped at three-day intervals for five successive dippings. In this manner, the number of ticks was steadily reduced, those which attached themselves being killed by dipping before they could complete engorgement. Care was taken to prevent extraneous contamination of either the central or neutral area: the sheep were transported in and out in a specially constructed solid walled carrier, and the experimenters were required to wear rubber knee-boots, which were washed in a tub of insecticide placed immediately inside the outer fence. After September 1930, the area was left vacant until the spring of 1932. Thus, from May 1929 until the beginning of the tick season of 1932, no ticks in the central area were able to feed on sheep and drop back on to the pasture. The individuals of the original tick population, *except those which fed on alternative hosts*, were either removed and killed by the repeated serial dippings, or starved to death for want of a blood meal.

At the end of September 1930, when the area had been subjected to three spells of intensive stocking and serial dipping, the number of ticks was considered to have been reduced to a minimum. For the succeeding eighteen months, the area was left untouched, to allow of the vermin- and bird-supported population attaining an equilibrium.

IV. RESULTS OF THE EXPERIMENT.

About the middle of April 1932, ten sheep, after being carefully dipped, were placed on the central area. Accurate counts were made every fourth or fifth day of the number of female and nymphal ticks attaching themselves to the head, neck and ears of five of these sheep. As a control, similar counts were made of the degree of infestation of twelve of a group of sheep pastured on the adjacent areas of tick-infested pastures. The results are shown in the table, and the comparative degrees of infestation per sheep in the two groups are represented in the accompanying graph (Fig. 1).

It will be seen that, although the degree of infestation was markedly

Comparative degree of infestation of sheep on experimental area and ordinary farm grazing.

	Controls					Experimental area				
Date	No. of sheep examined	♀♀	Nymphs	Total	Average per sheep	No. of sheep examined	♀♀	Nymphs	Total	Average per sheep
16. iv. 32	12	16	72	88	7	5	—	1	1	—
21. iv. 32	12	17	180	197	16	5	6	5	11	2
25. iv. 32	12	34	89	123	10	5	2	3	5	1
1. v. 32	12	50	180	230	19	5	10	23	33	6½
5. v. 32	12	31	98	129	11	5	9	18	27	5½
9. v. 32	12	42	204	246	21	5	2	2	4	1
14. v. 32	12	42	204	246	21	5	3	18	21	4
18. v. 32	12	72	468	540	45	5	2	20	22	4½
23. v. 32	12	56	204	260	22	5	4	24	28	5½

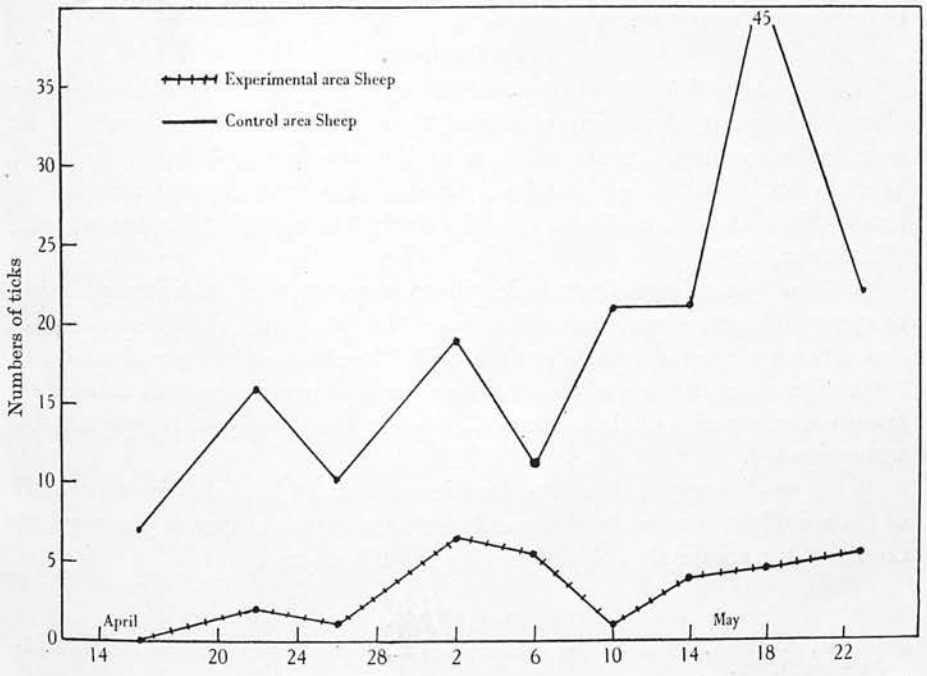

Fig. 1.

greater in the sheep grazing on the ordinary pasture, there was a regular and appreciable infestation of those sheep on the central area. The average degree of infestation of each group may be taken as a reflection of the comparative density of the tick population of the central area and of the ordinary pasture. The comparative density of stocking of the two areas during the experiment, although it would affect the result in the next generation of ticks, does not affect the immediate result, since a grazing sheep covers in a day a constant area of pasture irrespective of the density of stocking, and so the average infestation per sheep will remain constant. It would appear, therefore, that in the central area a tick population of appreciable size was maintained by ground vermin and birds, although no ticks on this area had engorged on sheep for the previous three years.

This result, apart from its important bearing on tick control measures, is of interest in that we have here a parasite which, although normally affecting one chief host, is able to maintain itself in appreciable numbers in the complete absence of that host. The result is the more striking in that the number of possible alternative hosts was very much reduced. Hares obtained access by virtue of their leaping powers; apart from them, the only mammals likely to have gained entry, and which are known to harbour ticks, were weasels and stoats. It is not known whether these ticks feed on mice and voles. The only other possible hosts were the common moor birds.

It is probable, therefore, that many of the more adaptable parasites with a comparatively wide host range are able to survive in the complete absence of their chief host or hosts.

V. Summary.

1. The sheep tick, *Ixodes ricinus*, feeds on a very wide range of hosts other than the sheep. As shown in a previous paper, these include the horse, cattle, deer, hedgehog, dog, fox, cat, stoat, weasel, ferret, hare, rabbit, rat, squirrel, hoodie crow, jackdaw, golden plover, barn owl, grouse, kestrel and merlin hawk. Since then, it has been recorded from the siskin and sparrowhawk, (Thompson, 1934).

2. In a 10-acre area, from which sheep were excluded, a tick population of appreciable extent was maintained where the only available hosts were birds and hares, and ground vermin such as field mice, voles, weasels and stoats.

3. The effect of these alternative hosts on the population was allowed to operate over a period of eighteen months before the density of the population was estimated.

4. It would appear, therefore, that in the case of *Ixodes ricinus*, removal of the chief host (sheep) from a particular area for a number of years would not effect the eradication of the parasite from that area.

References.

MacLeod, J. (1933). "Bionomics of *Ixodes ricinus* L., the 'sheep tick' of Scotland." Parasitology, 24, 382.

Thompson, G. B. (1934). Ent. Mon. Mag. **70**, 204.

IXODES RICINUS IN RELATION TO ITS PHYSICAL ENVIRONMENT: THE INFLUENCE OF CLIMATE ON DEVELOPMENT

BY

J. MACLEOD

FROM PARASITOLOGY, VOL. XXVI, NO. 2, 23 JUNE, 1934

CAMBRIDGE
AT THE UNIVERSITY PRESS

PRINTED IN GREAT BRITAIN

[From PARASITOLOGY, Vol. XXVI, No. 2, June, 1934.]

IXODES RICINUS IN RELATION TO ITS ENVIRONMENT: THE INFLUENCE OF C ON DEVELOPMENT

By J. MacLEOD

Carnegie Research Fellow, Moredun Institute, Edinl

(With 6 Figures in the Text)

CONTENTS

I. Introduction

During the last few decades, a considerable amount of experi been carried out on the relations of insects to their environ groups such studies have advanced to an extent which rend tative efforts at accurate prediction of their activities and spr arachnids, however, the experimental study of ecological r been almost entirely neglected, and this despite the fact tha especially among the mites and ticks, are of marked econo Since 1892–3, when the researches of Smith and Kilborne on cattle were published, ticks have been proved to be vect important diseases of man and animals in many parts of the

knowledge of their bionomics has been gained through observations conducted in the field and in the laboratory. The ecology of ticks under precisely controlled conditions, however, provides a practically unexplored field.

The only tick of major importance in Britain is *Ixodes ricinus*, which is the vector of redwater in cattle, and of louping-ill and tick-borne fever in sheep. In 1929 an investigation of its bionomics was begun by the writer, and, following its incrimination as the carrier of louping-ill and tick-borne fever, a comprehensive study of its general environmental relationships was undertaken. An account of certain field observations on its distribution, seasonal activities and host relationships has already been published (MacLeod, 1932).

The present paper describes laboratory experiments upon the effects and intereffects of different physical factors in the environmental complex on the development of gorged *Ixodes ricinus*, hereafter referred to merely as the tick or ticks.

II. Influence of temperature and humidity on development

(*a*) *Methods*

The ticks used in the experiments described below were bred for one or more generations in the laboratory. The methods of breeding have already been described (MacLeod, 1932).

For experiments at constant temperatures of 22·5° C. and over, ordinary gas-heated thermostats set at different temperatures were used. The temperature of each thermostat did not vary more than plus or minus half-a-degree Centigrade. There is a slight variation of temperature between different parts of thermostats of this type, but the possible error from this source may be obviated to a certain extent by keeping the tick containers as far as possible in the same position in the incubator for all experiments. A temperature of 20° C. was obtained by a water-bath with a gas-control mechanism, with the addition of the usual cold-water circulation for thermostats at 14–16° C. A portable electric incubator, kept in an outhouse in winter, provided a steady temperature of 10° C., while the cold store was used for the lowest temperature of 2–3° C. Constant humidities were obtained by using solutions of caustic potash, the relative humidity over which remains practically constant for given concentrations throughout the biological range of temperature (Paranjpe, 1918). Pure caustic potash sticks were used for making the solutions, and their anhydrous purity tested before use by titration of a given solution against standard hydrochloric acid. The ticks for each experiment were placed in a test-tube, the mouth of which was covered by muslin, held taut by a rubber band. Each tube was placed in a milk sample bottle containing some caustic potash solution of the requisite concentration, and the bottle tightly closed with a rubber stopper. After exposure of the system for some hours to the appropriate temperature, the stopper was released and replaced; thus a normal atmospheric pressure in the closed system was obtained. When the ticks approached the moulting stage the tubes were examined daily and the

number of moults recorded. In some of the experiments, where the ticks were left for 2 or more months over KOH solutions, there was a tendency for K_2CO_3 to form, through absorption of CO_2. This, however, would not appreciably affect the result since, according to Paranjpe, 2 g. K_2CO_3 equals 1·5 g. KOH, as far as vapour pressure is concerned.

(*b*) *Experimental data*

Two series of experiments with larvae, and three with nymphs, were carried out at different combinations of temperature and humidity. Four to eight gorged nymphs and ten gorged larvae were used in each experiment; the results recorded below have, therefore, been obtained from approximately twenty larvae and eighteen nymphs at each combination. The ticks in each series were submitted to experiment on the same day on which they had completed engorgement. The shortest, longest and average time (in days) from engorgement to moulting, and the percentage mortality are given in tabular form (Tables I and II).

Table I. *Larvae. The number of days taken for development, and the mortality at different temperatures and humidities.*

Relative humidity		Temperature °C. 22·5	26	27·5	30	32·5	35
100	Shortest	48	25	22	19	17	18
	Longest	64	37	34	25	22	28
	Average	56	31	28	23	20	21
	Mortality (%)	0	5	0	0	0	35
95	Shortest	34	28	24	22	19	22
	Longest	70	48	37	28	28	30
	Average	55	38	30	25	24	28
	Mortality (%)	15	15	20	20	10	90
90	Shortest	40	31	28	23	28	—
	Longest	70	54	37	32	31	—
	Average	58	41	32	26	29	—
	Mortality (%)	30	15	5	15	65	100
85	Shortest	51	40	34	23	—	—
	Longest	64	61	41	32	—	—
	Average	59	48	37	28	—	—
	Mortality (%)	55	50	80	85	100	—
80	Shortest	—	—	—	—	—	—
	Longest	—	—	—	—	—	—
	Average	—	—	—	—	—	—
	Mortality (%)	100	100	100	100	—	—

The following points in the tables are worthy of remark:

(1) There is a marked individual variation in the time taken for development; ticks of identical history, kept under similar conditions in the same tube, exhibited variations of as much as one-quarter or even one-third of the longest time recorded for these particular conditions.

(2) The lower limiting conditions of humidity for survival and development of gorged ticks is surprisingly high, being in the neighbourhood of 80 per cent. saturation at the lower medial temperatures, and 90–95 per cent. at the upper

temperatures. The larval stage appears to be even more intolerant of aridity than the nymphal stage, the lower limit at 22·5° C. being about 85 per cent.

(3) Under the same conditions of temperature and humidity, the gorged nymph required longer time for development than the gorged larva.

(4) There appears to be a higher mortality among nymphs than among larvae.

Table II. *Nymphs. The number of days taken for development, and the mortality at different temperatures and humidities.*

Relative humidity		Temperature °C. 22·5	25	27·5	30	32·5	35
100	Shortest	68	47	35	25	23	23
	Longest	86	74	47	33	31	30
	Average	78	61	41	30	28	28
	Mortality (%)	33	26	7	20	14	38
95	Shortest	—	46	31	27	28	30
	Longest	—	72	49	28	41	—
	Average	—	60	39	30	33	—
	Mortality (%)	—	0	0	30	13	50
90	Shortest	50	44	31	27	31	36
	Longest	59	72	47	36	40	—
	Average	55	49	37	31	38	—
	Mortality (%)	30	14	0	0	29	80
85	Shortest	72	55	40	32	31	—
	Longest	82	74	45	44	—	—
	Average	79	65	44	37	—	—
	Mortality (%)	30	0	43	0	50	100
80	Shortest	59?	—	39	34	—	—
	Longest	—	—	63	40	—	—
	Average	—	—	49	37	—	—
	Mortality (%)	88	100	50	63	100	—

(c) *Development at constant temperatures and humidities*

If the time taken for development of gorged larvae in saturated air is plotted against temperature, within the limits given in Table I, it will be seen that the curve is of the nature of a hyperbola (Fig. 1). In this respect it agrees with the general curve for insect development at medial temperatures.

The work of Peairs (1914), Bodenheimer (1928) and others has shown that the correlation curve between temperature and development of various insects is a true equilateral hyperbola for the medial temperature range, the product of the effective temperature and the time being a constant. The curve for tick development (Fig. 1) suggests that the law of thermal constants holds good for development of ticks also, within the medial temperature range. The application of the thermal-constant theory to the development curve will be discussed in detail later.

An examination of the data in Table I reveals the fact that the temperature at which development takes place most rapidly is not a fixed value irrespective of the humidity conditions, but varies with different humidities. If the reciprocal values of the time taken for development are plotted against temperature, the resulting curve represents the relative velocity of development

at different temperatures. In Fig. 2 the velocity-temperature curves of larva at 100, 95 and 90 per cent. saturation have been drawn. The curves are base on the shortest times for development (Table I). The curves illustrate thre points of interest.

(1) Saturated air affords the optimum moisture conditions for developmen at temperatures over 26° C., the velocity for any temperature over this de creasing with decreasing humidities. The greatest developmental velocit obtained was in saturated air.

(2) Under optimum humidity conditions, 32·5° C. appears to represe the temperature at which development proceeds most rapidly.

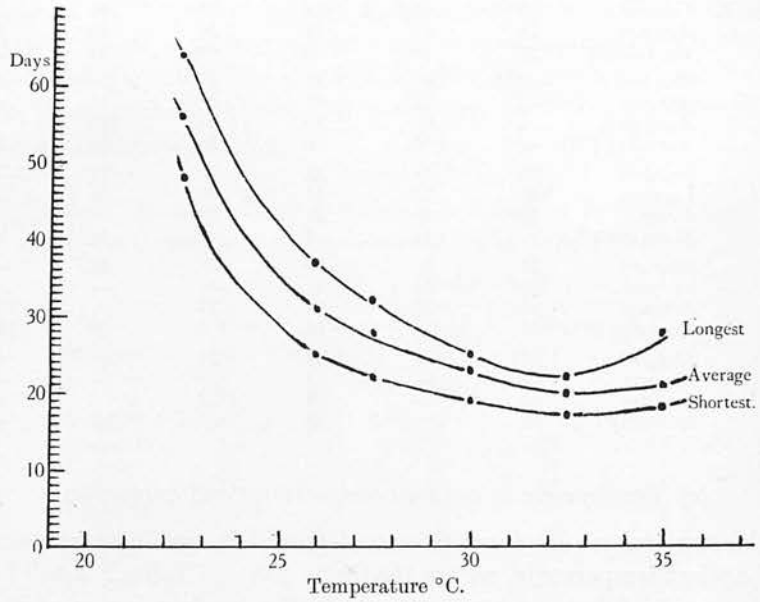

Fig. 1. Development curves of gorged larvae at different temperatures. Shortest, longest a average times for development (Table I).

(3) With decreasing humidities the point at which the greatest develo mental velocity is exhibited tends to move down the temperature scale; f 100 per cent. saturated air the difference between the velocity at 32·5° C. an that at 35° C. is insignificant; for 95 per cent. saturated air the velocity definitely greater at 32·5° C., while in air, 90 per cent. saturated, 30° C. the optimum temperature as regards velocity.

A study of Table II shows that the same general principles hold for de velopment of gorged nymphs, except that the velocity curve remains stationar from 32·5° to 35° C., instead of dropping slightly, as in the case of larvae.

It has been shown that the optimum temperature for development velocity is dependent on humidity. The converse of this also holds—th optimum humidity for development is dependent on temperature. This

more clearly illustrated in the case of the gorged nymphs. Fig. 3, giving the velocity-humidity curves of gorged nymphs at different temperatures, shows that with decreasing temperatures the point at which developmental velocity is greatest tends to move down the humidity scale; at 30° C. the optimum humidity for developmental velocity is 100 per cent. saturation, at 27·5° C. it is between 90 and 95 per cent., and at 25° C. it is 90 per cent.

The same principle operates in the case of larvae, the deviation of the optimum humidity from saturation beginning at temperatures below 26° C.

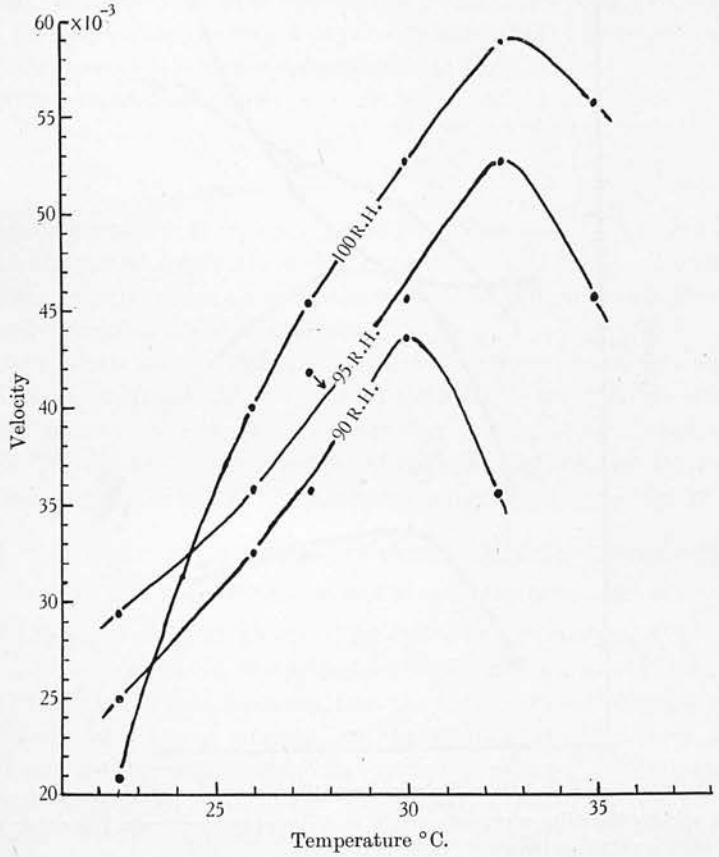

Fig. 2. The velocity-temperature curves of larvae at different humidities. The curves are based on the highest velocities obtained (Table I).

(*d*) *Development at fluctuating temperatures*

The recorded data on the influence of fluctuating temperatures on the development of insects is conflicting. Uvarov (1931) summarises the results of various workers, some of whom obtained a retardation, and others an acceleration effect by subjecting eggs and larvae of different insects to fluctuating temperatures. More recently, MacLagan (1932) found that violently fluctuating temperatures produced an initial acceleration in the rate

of growth of *Smynthurus* nymphs, but eventually proved harmful, resulting a rapid decrease in rate.

Other workers have studied the effect on the development of vario insects of preliminary exposures to high or low temperature, but this does n properly belong to the subject of fluctuating temperatures, and will be di cussed in relation to the tick in the next section. The effect of temperatu

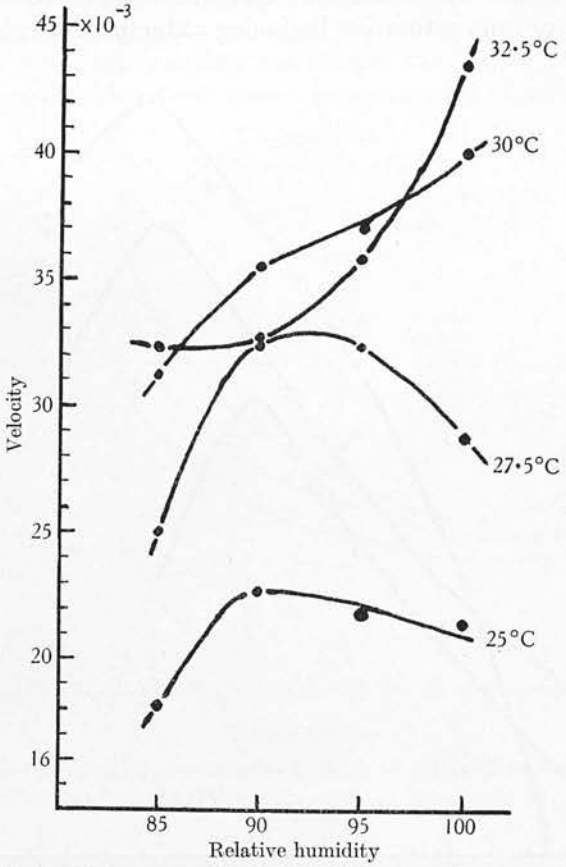

Fig. 3. The velocity-humidity curves of nymphs at different temperatures. The curves are bas on the highest velocities obtained (Table II).

fluctuations as these might occur in nature on the physiological response t particular temperatures is important, and must first be investigated before true conception can be formed of the influence of temperature as a climati factor, since organisms in nature are not subjected to the constant temperatur conditions obtaining in laboratory experimentation.

Gorged larvae which had been kept at room temperature for a few day were subjected to different temperatures as follows. Two control tubes, wit fifteen larvae in each, were exposed to 25° and 35° C. respectively. A third tube containing thirty larvae, was alternated every 3 days between 25° and 35° C.

To avoid the condensation of water on the bodies of the ticks, inevitable in saturated air when a tube is brought from 35° to 25° C., the experiment was carried out with a uniform R.H. of 95 in all the systems.

The results of the experiment may be summarised as follows:

The controls at 35° C. moulted from the 27th to the 30th day; those at 25° C. moulted from the 33rd day onwards; those exposed to fluctuating temperature moulted from the 33rd day onwards.

The experiment was repeated in saturated air, with narrower limits of fluctuation. Fifteen ticks were exposed to limits of 30° and 35° C., the temperature being alternated every 3 days. Control tubes of 10 larvae each were exposed to constant temperature conditions at these limits.

Moulting occurred as follows:

	Shortest	Average
Controls at 35° C.	19	22
Controls at 30° C.	20	25
Alternating tube	23	26

Violent fluctuations to extreme limits were then tested. A tube of twenty ticks was alternated every third day between 2° and 30° C. By the eighth alternation of temperature all the ticks were dead, probably as a result of the abrupt and violent changes of temperature.

It follows that, for the tick, moderate fluctuations of temperature within the favourable limits do not result in an appreciable acceleration of development; the results suggest that, if anything, a slight retardation effect is produced. The effect on development of maintaining the tick for periods of days at a succession of static temperatures is discussed in Section IV.

III. THE TEMPERATURE-VELOCITY CURVE AT FIXED TEMPERATURES

(*a*) *The possibility of stimulation by low temperatures*

Were the curve of development of the tick a true equilateral hyperbola, the reciprocal curve, expressing the velocity of development, would therefore be a straight line. It is obvious, however, that the curve of development throughout the full biological range of temperature cannot be a true hyperbola, since the tick will not survive indefinitely at low temperatures, and retardation of development and death occur at the upper limit. Prochnow (cited by Uvarov, 1931) traced the developmental velocity curve of various insects throughout the full temperature range, and found that above and below the medial temperature range the straight-line character of the curve was departed from. The method he adopted was to expose the insects for a certain interval at a low temperature, then to transfer them to a favourable temperature, and allow them to complete their development. The fraction of their development completed at the low temperature in the given time was reflected in the differences between the time required to complete development at the favourable temperature and the time required for total development at this temperature. From this the rate of development at the low temperature was calculated. The work of Bodine and Parker on the development of grasshopper

eggs (Uvarov, 1931) suggests a possible source of error in this method, however. These workers demonstrated that with grasshopper eggs a preliminary exposure to low temperature stimulated the eggs to a more rapid development at favourable temperature than would normally occur. The possibility, therefore, had to be considered that, if Prochnow's method were used to determine the velocity of development at low temperatures, results indicating an apparent development at the lower temperature might in reality be due to an acceleration of the normal rate at the higher temperature, resulting from the stimulative effect of the preliminary exposure. To test this possibility, the following experiment was set up.

Larvae were exposed to temperatures of 2–3° C. and 9–10° C. for a period of 60 days, then transferred to 27·5° C., R.H. 95. It was reasoned that, if genuine stimulation resulting in accelerated development had occurred, this would be at least as marked, if not more so, in the ticks exposed to 2–3° C. as in those exposed to 10° C.

Moulting occurred in both lots between the 31st and 37th day after removal to 27·5° C. The average time for complete development at 27·5° C. 95 R.H., is 30 days; it would appear, therefore, that, in so far as the tick is concerned, stimulation by exposure to low temperature does not produce an acceleration of developmental velocity at subsequent temperatures, but possibly a slight retardation.

It is, therefore, permissible, if the possibility of a slight degree of retardation occurring even at moderately low temperatures be disregarded, to use this method in the case of ticks to determine the velocity of development at temperatures below the medial temperature range.

(*b*) *Development at* 20° C.

An experiment was first set up in which gorged larvae were exposed at different humidities to a temperature of 20–21° C., and left until moulting commenced. One larva at R.H. 100 moulted on the 93rd day; at 90 R.H. two moults occurred on the 88th day, and at 85 R.H. two occurred by the 120th day. No further moults occurred.

The experiment was repeated, six nymphs and ten larvae being placed at 20° C. at each of the following relative humidities: 100, 95, 90, 85, 80 and 75. The results were as follows:

Table III

	Larvae		Nymphs	
Humidity	No. of moults	Time in days	No. of moults	Time in days
100	—	—	—	—
95	—	—	—	—
90	4	160–180	1 1	110 170
85	—	—	2 2	83–90 170
80	—	—	—	—
75	—	—	—	—

No further moulting had occurred by the 190th day. Practically all the remaining larvae were found to be dead. The surviving unmoulted nymphs were transferred on the 190th day to 27·5° C., 100 R.H.

Moulting occurred as follows:

Table IV. *Nymphs.*

R.H. when at 20°	100	95	90	80	75
No. of days at 27·5° C., 100 R.H.	4	7	4	10	13
	7	—	10	13	—
	10	—	10	—	—
	10	—	—	—	—
	10	—	—	—	—

Since the average time taken for complete development at 27·5° C., R.H. 100, is 41 days, the amount of development which took place in from 4 to 10 days represented approximately from 1/4 to 1/10 of the total. That is, in 190 days, the unmoulted nymphs at R.H.s of 100 and 90 had completed from 3/4 to 9/10 of their development, and, therefore, would theoretically require from about 20 to 60 more days. The shortest and longest periods for nymphs at 20° C., worked out from these results, are as follows:

R.H.	100	90	85	80	75
Shortest	210	110	83–90	250	280
Longest	250	250	170	280	—

Thus we find that at 20° C. the humidity at which development is most rapid is 85 per cent., the velocity decreasing at humidities above and below this point.

The developmental velocity of gorged larvae at this temperature was found as follows:

Tubes each containing ten larvae were set at 20° C., 100, 90 and 80 R.H. After exposure for 68 days they were removed. Those at 80 R.H. were found to be dead. The remaining two tubes were set at 27·5° C., 100 per cent. saturation. Moulting occurred as follows:

Table V. *Larvae.*

100 R.H.		90 R.H.	
No. of moults	Days at 27·5° C.	No. of moults	Days at 27·5° C.
1	7	2	7
3	10	1	10
3	13	1	17
3	17	Remainder died	

The time required by larvae at 27·5° C., 100 per cent., averages 28 days; that is, 7/28–17/28 of the total development was completed at 27·5° C. and, therefore, 68 days represents from 11/28 to 21/28 of the total number required at 20° C. This makes the time at 20° C. required by gorged larvae for complete development approximately 90–170 days. Combining this result with the

result of the first experiment, we find the time required for development gorged larvae at 20° C. to be as follows:

R.H.	100	90	85
Days	90–170	88–170	120–?

In these results, as in the results given in Tables I and II, there is a clea indication in the case of the nymph than in that of the larva of a deviation the optimum humidity from saturation with decreasing temperatures.

(c) *Development at temperatures of* 15° C. *and under*

Gorged larvae were exposed to the following combinations of humidity a low temperature:

Temperature ° C.	R.H.					
2–3	100,	90	—	—	—	—
10	100,	95,	90,	85	—	—
14–16	100,	95,	90,	85,	80,	75

2–3° C. The larvae at 2–3° C., 100 R.H., were transferred after 100 days 27·5° C., 95 R.H. (Those at 90 R.H. were found to be dead.) Moulting co menced on the 31st day.

10° C. The ticks at 10° C. were transferred to 27·5° C., 95 R.H., aft 85 days. Moulting began as follows:

100 R.H., 27 days; 95 R.H., 24 days;
90 R.H., 27 days; 85 R.H., 27 days.

14–16° C. The larvae at this temperature were transferred to 27·5° 95 R.H., after 100 days, and moulted as follows:

R.H.	100	95	90
Shortest	Dead	24	24
Average	—	29	—

Tubes each containing six gorged nymphs were exposed to a temperatu of 14–16° C., at R.H.s of 100, 95, 90 and 80, left for 100 days and then tra ferred to 27·5° C., 95 R.H.

Moulting occurred as follows:

R.H.	100	95	90	80
Shortest	Destroyed by accident	32	31	26
Average	—	34	32	31

Since the shortest and average periods for total development at 27·5° C 95 R.H., are 24 and 30 days (larvae), and 31 and 39 days (nymphs), it follo from these results that, at temperatures of 14–16° C. or below, there is n appreciable development after exposures for periods of 85 and 100 days.

An unusual feature of all the results with low-temperature experimen was the high mortality among the ticks. Even at 20° C. the majority of th nymphs and larvae exposed for long periods died. It is not known whethe this was due to changes in the gaseous contents of the closed systems duri these prolonged periods, to changes in the moisture conditions as a result o absorption of CO_2 by the KOH solutions, or to the effect of exposure to a unchanging temperature unfavourable for rapid development.

Several att
at 37·5° C., va
An effort was
removing the
them to comp
ten larvae eac
to 30° C. afte
three tubes die
for developme
definitely unfa

From the
of ticks can b
Fig. 4, veloci

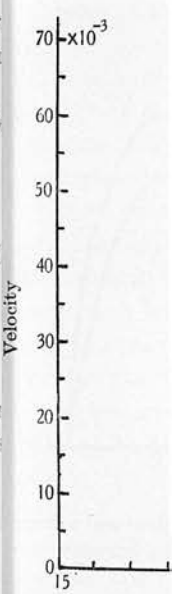

Fig. 4. The veloc
in saturated

against tempe
taken in satur
within the lim
above and be
peratures ove
very steeply t
be a slight rel
the threshold

(*d*) *Development at temperatures of over* 35° C.

Several attempts were made to induce both larvae and nymphs to develop at 37·5° C., various humidities being used, but in every case the ticks died. An effort was then made to find the rate of development at this temperature by removing the ticks before the lethal effect had time to operate, and allowing them to complete their development at a lower temperature. Three tubes of ten larvae each were set at 37·5° C. in saturated air; one tube was removed to 30° C. after 5 days, one after 10, and one after 15 days. The larvae in all three tubes died. It would appear, therefore, that the upper limit of temperature for development lies between 35 and 37·5° C., the latter temperature being definitely unfavourable even when ticks are exposed to it for only a few days.

From the foregoing experimental results, the developmental velocity curve of ticks can be produced above and below the medial temperature range. In Fig. 4, velocity curves of development of gorged larvae have been plotted

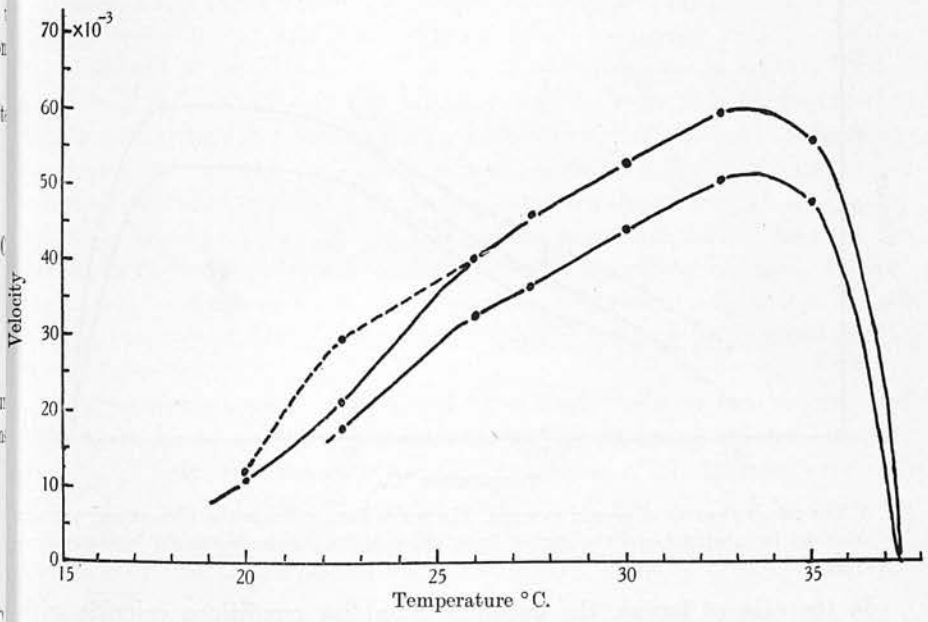

Fig. 4. The velocity curve of gorged larvae, based on the highest and average velocities obtained in saturated air. The broken line represents the highest velocity at optimum humidities.

against temperature, the curves being based on the shortest and average times taken in saturated air at different temperatures. It will be seen that, although within the limits of 26 and 32·5° C., the curve is approximately a straight line; above and below these limits the character of the curve alters. At temperatures over 32·5° C., the curve tends to fall away, at first slightly, and then very steeply to zero velocity at 37·5° C. Below 26° C. there would appear to be a slight relative retardation of development with decreasing temperatures, the threshold of development lying in the neighbourhood of 15° C.

An interesting point raised by the above findings is the question of t
correct humidity to be considered when plotting full velocity curves. It l
been shown above that the humidity conditions under which developm
proceeds most rapidly are not the same for all temperatures. Where t
"optimum" humidity is below saturation, one may reasonably assume th
conditions either more or less humid than the optimum exercise an inhibit
influence which retards the velocity rate. It would, therefore, appear to
more accurate to take the optimum humidity for each temperature, rather th
a constant condition, *e.g.* saturation, when plotting a velocity curve rep
senting the response of an organism to temperature alone. Otherwise, t
curve is not a true reflection of the response evoked by temperature, since
certain temperatures the result obtained represents the response after modi
cation by the retardation effect of unfavourable humidity.

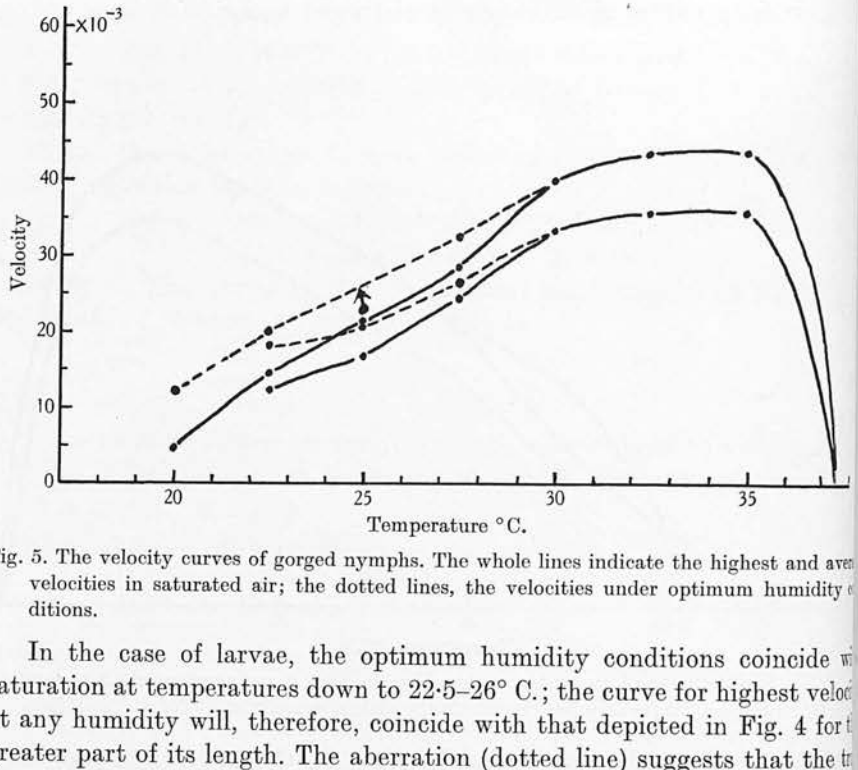

Fig. 5. The velocity curves of gorged nymphs. The whole lines indicate the highest and aver
velocities in saturated air; the dotted lines, the velocities under optimum humidity c
ditions.

In the case of larvae, the optimum humidity conditions coincide wi
saturation at temperatures down to 22·5–26° C.; the curve for highest veloc
at any humidity will, therefore, coincide with that depicted in Fig. 4 for t
greater part of its length. The aberration (dotted line) suggests that the tr
velocity curve retains its straight line character down to 22·5° C. befo
exhibiting deceleration. On the other hand, as shown in Table II, the optimu
humidity for gorged nymphs departs from saturation conditions at high
temperatures. Fig. 5 depicts the velocity curves for gorged nymphs be
under constant saturated air conditions and at optimum humidities. It
clear from this figure that the velocity curve under a constant humidi
condition may be misleading; the curves for saturated air (unbroken lines) a

irregular, whereas those for optimum moisture conditions (broken lines) exhibit the conventional straight-line character for medial temperatures.

(e) *The threshold of development and the thermal-constant theory*

As has been pointed out above, when the reciprocals of the times taken for development are plotted against temperature, the resulting curve expresses the velocity of development. Where this curve transects the temperature axis the velocity is zero, and this temperature represents the theoretical threshold of development. Many workers have obtained this point by producing the reciprocal of the development curve at medial temperatures, on the assumption that the development curve is a hyperbola and its reciprocal, therefore, a straight line. It is now generally admitted, however, that the hyperbolic zero is only an approximate indication of the threshold of development.

If the development curve be admitted a hyperbola, the product of the ordinates of any point will be a constant. The ordinates in such a case are the time for development and the number of effective degrees, or degrees above the threshold of development. That is, development would require a fixed number of day-degrees, or the principle may be expressed by saying that exposure for x days at a temperature y degrees over the threshold has the same developmental effect on the organism as exposure for y days at a temperature x degrees over the threshold. This thermal-constant theory is much used to-day by insect ecologists, but it has the serious objection that it assumes the development curve to be a hyperbola, whereas the curves of insect development have been shown to be represented by hyperbolae only within limited temperature ranges. It is of interest to apply the theory to the development curve of the tick.

A development curve represented by a true hyperbola can be expressed by the formula $xy=c$, where y is the time for development, and x the number of effective degrees of temperature. The value x may be expressed as $T-K$, where K is the threshold of development, and T the recorded temperature. Since C, the thermal constant, is fixed, the value K may be obtained if the ordinates of two points on the curve are known. Thus, if $(T-K)\ Y=C$ and $(T_1-K)\ Y_1=C$, then

$$K=\frac{TY-T_1Y_1}{Y-Y_1}.$$

Taking the results given in Table I, we find that K has the following calculated values:

Temperatures °C.		K °C.
22·5	26	20
22·5	27·5	18
26	27·5	15
26	30	13
27·5	30	12
27·5	32·5	10
30	32·5	9

It follows, therefore, since K is not a constant value, that the full devel mental velocity curve cannot be expressed as a hyperbola; that is, each d degree has not a uniform developmental value.

It is apparent, therefore, that the thermal-constant theory cannot sa be used here as a basis for calculating the threshold of development.

IV. The temperature-velocity relation with varying temperatures

It has been shown that a day-degree has not a fixed developmental va but varies with different temperatures. It now remains to be seen whether, temperature being fixed, the application of a fixed number of day-deg produces a constant developmental response, or whether the intensity response is subject to variation according to the previous history of organism. It has been shown that exposure to a temperature well below threshold of development appears to produce a slight retardation in response to a subsequent favourable temperature; there remains the possibil that exposure for a period to one temperature within the favourable limits m affect the velocity of development when the organism is later subjected another favourable temperature.

Two tubes each containing ten fully gorged larvae were set at 25° and 35° respectively, each under optimum humidity conditions, *i.e.* saturation.

After exposure for 12 days, the tubes were interchanged and left u moulting was completed.

The results were as follows:

Table VI. *Larvae.*

	First temp. ° C.	Period exposed days	Second temp. ° C.	Shortest time	Avera time
Ticks exposed to successively lower temperatures	25	12	35	10	12
Ticks exposed to successively higher temperatures	35	12	25	12	15

The velocity values for 25° and 35° C. when the ticks are exposed t fixed temperature throughout their development may be obtained from velocity curve (Fig. 4) by interpolation in the case of 25° C., and by di reading for 35° C.

They are: 25° C. Highest, 1/27. Average, 1/33.
35° C. Highest, 1/18. Average, 1/21.

Let x = velocity at 25°, x_1 that at 35° C. Thus

$$\frac{x}{x_1}=\frac{18}{27}=\frac{2}{3} \quad \text{(highest)};$$

or

$$=\frac{21}{33}=\frac{7}{11} \quad \text{(average)}.$$

Applying these ratios to the above results, we find that the calculated times for development at the second temperature in each case should be as follows:

Rising temperatures:

Development at 35° C. = 18 − 2/3 of 12 = 10 days at 35° C. (highest velocity);
or 21 − 7/11 of 12 = 13 days (average velocity).

Falling temperatures:

Development at 25° C. = 27 − 3/2 of 12 = 9 days at 25° C. (highest velocity);
or 33 − 11/7 of 12 = 14 days (average velocity).

These theoretical results compare with the observed results as follows:

Falling temperatures				Rising temperatures			
Observed		Calculated		Observed		Calculated	
12	15	9	14	10	12	10	13

There is no significant difference between the observed and calculated results.

It follows, therefore, that, humidity conditions being uniformly optimum, unit exposure to a fixed temperature has a fixed developmental effect, irrespective of the previous history of the organism in regard to temperature, except where this involves exposure to lethal high temperatures, or to very low temperatures.

This quantitative agreement between temperature and velocity is of interest in view of a recent paper by Falke (1931). This author stated that development of *Ixodes ricinus* underwent in the winter months an interruption which could not be altered by the employment of favourable conditions. He suggested that development may be divided into two phases, the *Vorruhestadium*, which lasts for 2 or 3 days, and during which the ticks are active, and the *Ruhestadium*, or stage of inactivity. Ticks which have not reached the *Ruhestadium*, or resting stage, at the onset of winter conditions cannot do so until the spring, and thus overwintering of gorged ticks occurs. Once the resting state is reached, the rate of development exhibits no appreciable variation, development occupying approximately 25 days.

Were this the case, exposure at different temperatures during the resting stage would not affect the velocity of development, provided the ticks were exposed to an initial fixed temperature during their pre-resting stage. That is, ticks exposed to an initial temperature of, say, 25° C., would complete development in a fixed time irrespective of whether they were removed to another temperature a few days later, or left at 25° C. The experimental results described above show that this is not the case. Further, since many of the experiments described in this paper were carried out in winter, it follows that, in this country at any rate, there is no seasonal diapause, such as Falke suggests, in the physiological activity of the tick.

V. Intereffects of temperature and humidity variations

The previous section dealt with the effects of temperature and humidit individually, variations in one factor being considered under conditions whe the other factor was constant. In nature, however, both factors operate a variables simultaneously; their intereffects and the effect of their simultaneo variations must, therefore, be considered.

It can be shown theoretically, from an analysis of the data obtained und constant conditions, that each factor intimately affects the potentiality of th other. If we consider the moisture conditions in the different experiments i terms of vapour pressure, we obtain a common vehicle of expression for bot the temperature and the humidity factor. It is known that, temperatu being constant, saturation deficiency varies inversely with the relati humidity, and can be calculated if the latter is known; humidity being co stant, saturation deficiency varies directly with the temperature, and can b

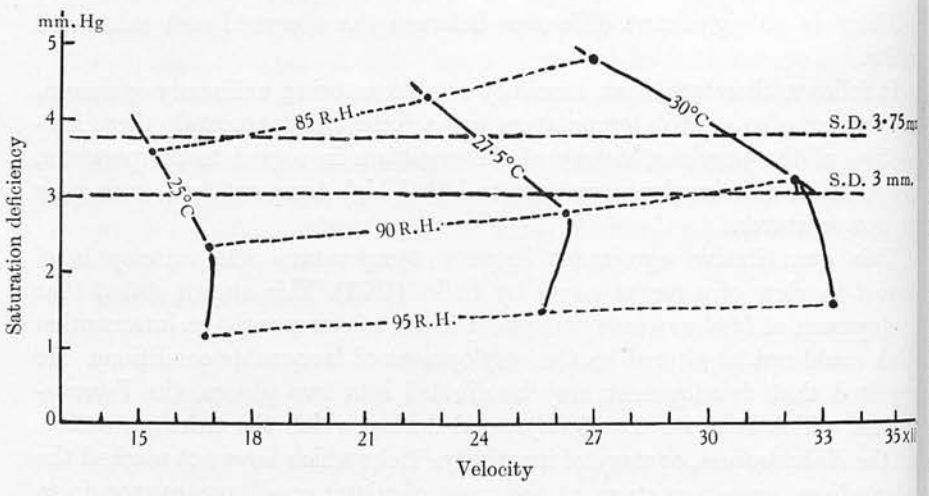

Fig. 6. Intereffects of temperature and humidity. The dotted lines represent the effect on develo mental velocity of temperature variations at different humidities; the whole lines, the effe on velocity of relative humidity variations at different temperatures. The parts of the curv enclosed by the interrupted lines indicate the comparative velocity response at differe temperatures to an absolute humidity increment (3·75 to 3 mm. deficiency).

calculated if the latter is known. It follows that, since saturation deficienc is a function of both relative humidity and of temperature, if developmenta velocity be plotted against saturation deficiency, the resulting curves wi illustrate the influence of temperature on the humidity effect, and the influen of humidity on the temperature effect.

In Fig. 6 the average velocity of development of gorged nymphs has bee plotted against saturation deficiency, and the resulting curves illustrate th intereffects of the two factors. The dotted lines represent the effect on velocit of temperature variations at different relative humidities; the whole lines, th

effect on velocity of relative humidity variations at different temperatures, as follows:

(*a*) *The effect of a particular humidity change at different temperatures*

It will be seen that at all three temperatures there is an increasing velocity with decreasing saturation deficiency, *i.e.* with increasing humidity, up to a point, after which the influence of humidity on temperature response becomes less marked or even reversed. This principle has already been encountered (Fig. 3). If those limits of saturation deficiency be considered within which the responses at all temperatures are qualitatively similar, *i.e.* saturation deficiencies of 3–3·75 mm., the curves demonstrate a quantitative agreement between saturation deficiency and temperature response. Thus a decrease of absolute humidity from 3 to 3·75 mm. deficiency in the vapour pressure is equivalent to the following velocity retardations at different temperatures:

25° C., velocity retarded by	10/161	or 6·2 per cent.
27·5° C., ,, ,,	18/258	or 7 per cent.
30° C., ,, ,,	19/323 to 25/329	or 5·9–7·9 per cent.

There is no evidence here of a significant variation in the percentage reduction of velocity at the different temperatures; that is, at saturation deficiencies of 3 mm. or over, removal of a definite quantity of moisture from the air apparently retards development by an approximately fixed percentage, irrespective of temperature, *i.e.* irrespective of the total amount of moisture in the air.

Since a fixed quantity of moisture at different temperatures represents different proportions of the total amount present, it follows that a fixed change in velocity is produced at different temperatures by different degrees of change in the relative humidity. The converse of this is illustrated in the diagram, where a fixed change in degree of humidity produces different velocity retardation effects at different temperatures, *e.g.* R.H. reduced from 90 to 85 retards velocity:

At 25° C.	by 15/169	or 9 per cent.
At 27·5° C.	,, 36/263	,, 13·7 ,,
At 30° C.	,, 53/323	,, 16·4 ,,

It would appear, therefore, that there is a differential response to relative humidity variation at different temperatures, a greater response being evoked by the same percentage variation of humidity at high temperatures than at low. This does not hold in saturated air.

(*b*) *The effect of a particular temperature change at different humidities*

A decrease of temperature from 30° to 25° C. retards velocity by the following percentages at different humidity conditions:

Saturation deficiency	R.H.	Percentage retardation
Between 1 and 2 mm.	About 95	50
,, 2 ,, 3 ,,	,, 90	47
,, 3 ,, 4 ,,	,, 85	43

The regular trend of these results suggests that there may be a different response to temperature variation at different conditions of humidity, t response being greater at higher humidities. This would appear to hold go up to complete saturation of the air.

(c) *Simultaneous variations in temperature and humidity*

The effects of different static conditions of one factor on the respon evoked by variations in the other have been discussed. The intereffects of t simultaneous operation of variations in both factors remain to be consider and have been subjected to experimental analysis.

A number of tubes each containing ten newly gorged larvae were expos to different combinations of temperature and humidity, as follows: One ser of three tubes was exposed to progressively higher temperatures and humidit for different periods, and the time taken to moult under the last set of co ditions observed. The second series was exposed to progressively lower te peratures and humidities, and the times taken to moult observed.

The experiment and results may be tabulated as follows:

Table VII. *Larvae.*

					35° C., 100 R.H.	
Series 1:	Tube	25° C., 90 R.H.		30° C., 95 R.H.	Shortest	Averag
ascending temperatures	1	10 days		10 days	10 days	15 day
	2	15 ,,		5 ,,	13 ,,	14 ,,
	3	5 ,,		15 ,,	9 ,,	? ,,
Series 2:		Shortest	Average			
descending temperatures	1	2 days	6 days	10 days	10 days	
	2	0 ,,	3 ,,	5 ,,	15 ,,	
	3	8 ,,	9 ,,	15 ,,	5 ,,	

These observed results were compared with the results calculated from t data in Table I (the value for 25° C., 90 R.H., being obtained by interpolatio

The control values are:

35° C.,	100	R.H.	Shortest,	18.	Average,	21.
30° C.,	95	,,	,,	22.	,,	25.
25° C.,	90	,,	,,	32.	,,	43.

Tube 1 on the ascending scale may be taken to exemplify the method calculation.

Let x = shortest number of days at 35° C., and let complete develo ment = unity.

Thus
$$\frac{10}{32}+\frac{10}{22}+\frac{x}{18}=1;$$

$$\frac{x}{18}=1-\frac{10}{32}-\frac{10}{22}=\frac{41}{176};$$

i.e.
$$x=4.$$

Similarly, if x = average number of days at 35° C.,

$$\frac{10}{43}+\frac{10}{25}+\frac{x}{21}=1,$$

or $$x=7\text{–}8 \text{ days.}$$

Table VIII compares the observed and calculated results for the two series.

Table VIII

			35° C., 100 R.H.			
			Observed		Calculated	
Series 1	25° C., 90 R.H.	30° C., 95 R.H.				
Tube 1	10	10	10	15	4	7–8
„ 2	15	5	13	14	5–6	9–10
„ 3	5	15	9	?	2–3	6
			25° C., 90 R.H.			
			Observed		Calculated	
Series 2	35° C., 100 R.H.	30° C., 95 R.H.				
Tube 1	10	10	2–3	7	0	5
„ 2	15	5	0	3	0	3–4
„ 3	5	15	8	9	1	6–7

It will be seen that, in comparison with the temperature-velocity relation under optimum-humidity conditions (Table VI), there is here an appreciable discrepancy between the observed and calculated results. When the organism is exposed to different temperatures, and at the same time subjected to adverse humidity conditions of varying intensity, there is an apparent reduction in the degree of response to temperature increase.

Another experiment was set up, in which the moisture conditions were more severely unfavourable. A tube of twenty newly gorged larvae was exposed to 25° C., 85 R.H. After 6 days it was transferred to 30° C., 100 R.H. The first moult occurred on the 16th day of exposure to the last combination. Owing to a subsequent high mortality from mould, it was not possible to determine the average time taken. If, however, the shortest time at 35° C., 100 R.H., is calculated, from the equation $\frac{6}{41}+\frac{8}{23}+\frac{x}{18}=1$, it will be seen that x, the theoretical time required at 35° C., is 9 days. The actual shortest time recorded was 16 days. This supports the results of the previous experiment.

There is a suggestion also, from the results given in Table VIII, Series 2, although the figures are not so striking as those in Series 1, that a reduction of temperature under unfavourable moisture conditions imposes a severer check on development than would theoretically be expected. Except in Tube 3, however, the differences are too slight to be regarded as significant.

Since it has been shown (Section IV) that, under constantly favourable humidity conditions, temperature has a uniform quantitative effect on development, it follows that the apparent differences in the quantitative effect of particular temperatures in these experiments are due to the inhibitory effect of adverse humidity conditions. Whatever be the correct interpretation of this inhibitory effect, it is evident that humidity has an intimate controlling

influence on the responsiveness of the organism to temperature variations; would also appear that the intensity of operation of this retarding influen varies with the degree of departure of these factors from the optimum, t relation being direct in the case of humidity, and inverse in the case of te perature. Thus, the discrepancy is more marked in Series 1 than in Series the ticks in this series were exposed for relatively longer periods to high, optimum, temperatures than those in Series 2. Further, in Series 1, where t discrepancies are well marked, it will be seen that they are more pronoun in the case of the ticks exposed for 10 and 15 days to a relatively low humidi than in the case of those exposed to this humidity for only 5 days.

VI. Influence of barometric pressure on development and ecdysis

(*a*) *Influence of pressure on development*

The available evidence on the influence of barometric pressure on devel ment of arthropods is, as is indeed the case with other climatic factors, all relation to insects. The evidence suggests that insects are capable of tolerati wider variations of pressure conditions than would normally occur in natu The rate of development also of insects is apparently insusceptible of alterati in response to atmospheric pressure variations, even of a high order (Uvar 1931), although some workers have obtained a quickening of developm under constant conditions of reduced pressure. In view of these findings, t following unexpected results with gorged ticks are of interest.

Gorged larvae when a few days old were exposed at 30° C. in saturated to pressures of 10 and 5 lb. over normal, to normal atmospheric pressure, a to 5 and 8 lb. under normal, one tube of ten larvae being exposed to e condition.

The pressure conditions were obtained as follows: The stopper of e closed humidity system was pierced with two pieces of glass tubing, o which were fitted pieces of rubber tubing. Reduced pressures were obtai by aspiration from one tube, the pressure being recorded on a vacuum ga inserted into the other. Increased pressures were obtained by means of ordinary pump, fitted with a valve, the pressure being recorded on a press gauge. The tubes were then tightly clamped, and the stoppers, which were t down securely, were sealed with paraffin wax.

Moulting commenced in the control tube at normal pressure (N) on t 18th day. Two days later the experimental systems were opened, and t larvae examined for moulting.

Pressure	$N + 10$ lb.	10 moults
,,	$N + 5$ lb.	7 ,,
,,	N	8 ,,
,,	$N - 5$ lb.	Nil
,,	$N - 8$ lb.	Nil

The experiment was repeated, larvae gorged 4 days previously being set, twenty to a tube, at pressures of $N+(10–12$ lb.), $N+(6–7$ lb.), N, $N-5$ lb. and $N-(7–8$ lb.).

The first moult occurred in the controls on the 18th day, whereupon the other systems were examined.

Pressure	$N+10–12$ lb.	All 20 had moulted
,,	$N+6–7$ lb.	19 moults
,,	N	1 moult
,,	$N-5$ lb.	Nil
,,	$N-7–8$ lb.	Nil

The reduced pressure systems, which had not been opened, were left for another fortnight, during which no moulting occurred. The ticks in these systems were then removed to normal pressure at 27·5° C., 100 R.H. On examination a few days later, they were found to be dead.

It appears, therefore, that in the case of *Ixodes ricinus* development can be accelerated by increased pressure, and inhibited, or at least markedly retarded, by reduced pressures, the ticks actually being killed by prolonged exposures to pressures of 5 lb. or more under normal.

The experimental pressure variations used, however, were of a much greater order than would normally occur in nature, and there is no evidence for supposing that slight fluctuations, such as occur naturally, produce appreciable effects on development.

(*b*) *Influence of pressure on ecdysis*

Pictet (cited by Uvarov, 1931) concluded from his work on butterfly pupae that emergence took place as a result of a fall in barometric pressure altering the ratio between the pressure of the body fluids and that of the outer air. The wide limits of variation for individual moulting of ticks kept under identical conditions, when these were static (Tables I and II), suggested that this hypothesis might be applicable to ticks. The results of the following experiments, however, lend no support to this view.

Sixty larvae were kept at 30° C., 100 R.H., until moulting had commenced. They were then removed and forty of the remaining unmoulted larvae, presumably near the point of hatching, were divided into four lots of ten, and exposed to (1) a pressure of $N+5$ lb., (2) a pressure of $N-3$ lb., (3) a pressure which fluctuated between these two limits, and (4) normal pressure.

The tubes were examined for each of the following 5 days, without the systems being opened. By the 5th day moulting was completed among those set at increased, normal and fluctuating pressures, no appreciable difference being observed in the rates of moulting. In the tube exposed to reduced pressure, no moulting occurred by the 2nd day, when the system accidentally broke down.

The experiment was repeated; five tubes of twenty larvae each were kept at 30° C., 100 R.H., until moulting commenced. The tubes on examination were found to contain nineteen, nineteen, nineteen, eighteen and fifteen

unmoulted ticks respectively. The last tube was discarded, and the other f
set at (1) $N+7$ lb., (2) $N-5$ lb., (3) normal, and (4) a pressure fluctuating da
from $N+7$ to $N-5$ lb., commencing with $N+7$ lb. The result was as follo

Pressure	3rd day	7th day
Control	6 moults	11 moults
Positive pressure	8 ,,	17 ,,
Negative pressure	3 ,,	6 ,,
Fluctuating pressure	7 ,,	Discontinued

It will be seen that, if anything, a retardation of ecdysis results fro
reduction of barometric pressure. The pressure reduction in this case, howe
is greater than would occur in nature, and it is probable that, as regards
tick, normal barometric variations exercise no acceleration or inhibition ef
on ecdysis.

VII. Discussion

From a review of the foregoing experimental results, some concepti
of the relation of the developing tick to the main climatic factors affect
it may be formulated. It is clear that the two outstanding factors influen
development are temperature and moisture, and these appear to be import
both in their separate and their combined effects.

An interesting feature of the results is the wide range of temperature o
which development, at a greater or lesser rate, is possible. From a lower li
in the region of 15° C. to an upper limit of 35° C., development is appreci
although the velocity varies greatly between these extremes. Even m
striking is the comparatively small range of humidity conditions within wh
survival and development are possible, the tick in this respect differ
markedly from the majority of insects. Its lower favourable limit is 80–85
cent. saturation, while, for the greater part of the temperature range favour
for comparatively rapid development, the optimum moisture conditio
saturation vapour pressure.

In addition to this direct limiting effect, humidity also exercises a profo
influence on the response of the tick to temperature. Under static condition
both factors, the velocity of development is slowed down by subopti
humidity conditions. Further, the quantitative response of the organism
temperature variation is affected by variations of the humidity factor.

It is clear from a consideration of the mortality percentages at differ
temperatures that the optimum temperature for development is not sim
that temperature at which development proceeds most rapidly. Peairs (19
defines the optimum for insects as that temperature range within which
relatively greatest percentage of individuals accomplish their developm
within the relatively shortest period. Before the ideal optimum could
decided, the comparative value to the race of unit time-shortening and of
individual would need to be known, for it is conceivable that percent
mortality, up to a certain point, is sufficiently compensated by the decreas
the time spent in the inactive, non-parasitic phase.

Theoretically, the greatest efficiency would be found at that temperat

at which the highest velocity was reached under optimum humidity conditions, provided all survived, *i.e.* optimum would equal 100 per cent. survival, multiplied by the highest velocity. The actual efficiency at this temperature would, therefore, be the product of the percentage survival and the velocity, the whole expressed as a percentage of the theoretical optimum. Similarly, the efficiency at any temperature might be calculated. Thus, in the case of gorged larvae, the theoretical optimum is 32·5° C., at which temperature the average velocity is 1/20. The theoretical optimum efficiency, therefore, is $100 \times 1/20$ or 5.

The actual moulting efficiency for larvae

$$\text{at } 32{\cdot}5^\circ \text{ C.} = \frac{\text{percentage survival} \times \text{velocity} \times 100}{\text{theoretical optimum efficiency}} = 100 \text{ per cent.};$$

$$\text{at } 35^\circ \text{ C.} = 65 \times \frac{1}{21} \times 100 \times \frac{1}{5} = 62 \text{ per cent.};$$

$$\text{at } 30^\circ \text{ C.} = 100 \times \frac{1}{23} \times 100 \times \frac{1}{5} = 87 \text{ per cent.}$$

Thus, if we compare the product of the percentage survival and the velocity at each temperature with a theoretical optimum efficiency, we can obtain a relative scale of values for the "moulting efficiency" at different temperatures. In the case of larvae it would appear from the results in Table I that the efficiency curve exhibits a sharp peak at the optimum temperature of 32·5° C., but it is very doubtful if this result would be maintained over a wider series of experiments. More probably an increasing percentage mortality would accompany increasing temperatures, especially at 30° C. and over, since in nature such temperatures are not usually attained in moist soil—the normal habitat of the gorged tick. In Table II also the results are based on too small numbers, and, consequently, the mortality values are too irregular to allow of an accurate interpretation of the relative "moulting efficiency" of different temperatures.

ACKNOWLEDGMENTS. The work described above has been carried out for the greater part while the writer was entomologist to the Animal Diseases Research Association, Edinburgh. To that body, and especially to the Director of the Research Institute, Dr J. Russell Greig, he is indebted for much material aid and facilities for the investigation. Thanks are also due to Dr A. E. Cameron and to Prof. J. H. Ashworth for their careful reading and criticism of the manuscript, and to Dr P. A. Buxton for a full abstract of Paranjpe's paper, and for much valuable advice on control of humidity conditions.

REFERENCES

BODENHEIMER, F. S. (1928). *Biol. Zbl.* **48**, 714.
FALKE, H. (1931). *Z. Morph. u. oekol. Tiere*, **21**, 567.
MACLAGAN, D. S. (1932). *Bull. Ent. Res.* **23**, 101.
MACLEOD, J. (1932). *Parasitology*, **24**, 382.
PARANJPE, G. R. (1918). *J. Ind. Inst. Sci.* **2**, 59.
PEAIRS, L. M. (1914). *J. Econ. Ent.* **7**, 174.
—— (1927). *Bull. West Virginia Univ. Agric. Exp. Sta.* No. 208.
UVAROV, B. P. (1931). *Trans. Ent. Soc. Lond.* **79**, 1.

(*MS. received for publication* 8. XI. 1933.—Ed.)

PARASITOLOGY is published about four times a year. The numbers afterwards are issued in volumes each containing four numbers.

Papers for publication should be sent to THE EDITORS OF PARASITOLOGY, Molteno Institute, Downing Street, Cambridge. Other communications should be addressed to the University Press, Cambridge.

Papers forwarded to the Editors for publication are understood to be offered to *PARASITOLOGY* alone, unless the contrary is stated.

Contributors receive twenty-five copies of their papers free. Additional copies, not exceeding 100 (except in special cases), may be had at cost price: these should be ordered when the final proof is returned.

The subscription price is £2. 15*s*. per volume (post-free), payable in advance; single numbers 18*s*. 6*d*. net (double number 37*s*. net). Subscriptions may be sent to any Bookseller, or to The Cambridge University Press, Fetter Lane, London, E.C. 4.

The Cambridge University Press has appointed the University of Chicago Press agent for the sale of *Parasitology* in the United States of America.

IXODES RICINUS IN RELATION TO ITS PHYSICAL ENVIRONMENT

II. THE FACTORS GOVERNING SURVIVAL AND ACTIVITY

BY

JOHN MACLEOD

FROM PARASITOLOGY, VOL. XXVII NO. 1, 11 MARCH, 1935

CAMBRIDGE
AT THE UNIVERSITY PRESS

PRINTED IN GREAT BRITAIN

[From PARASITOLOGY, Vol. XXVII, No. 1, 11 March, 1935.]

IXODES RICINUS IN RELATION TO ITS PHYSICAL ENVIRONMENT

II. THE FACTORS GOVERNING SURVIVAL AND ACTIVITY

By JOHN MacLEOD

Carnegie Research Fellow, Moredun Institute, Edinburgh

(With 8 Figures in the Text)

CONTENTS

In a previous paper (MacLeod, 1934) the different physical factors in the environmental complex of the sheep tick were discussed in their relation to the development of the gorged tick, and an experimental analysis was made of the effects produced, under laboratory conditions, by their action and interaction. The present paper deals with the active unfed ticks. These present rather a different problem from the gorged ticks, for, whereas in their case the climatic optimum resolved itself into that combination of conditions under which development proceeded favourably and with a low attendant mortality, the unfed tick, on the other hand, is faced with two desiderata, survival and host-parasitisation, the physical optima for which may not be coincident. It is necessary, therefore, to consider not only the climatic optimum for survival and activity, but also the factor or factors which influence parasitisation, and those conditions under which host-parasitisation is facilitated.

The methods used for controlling temperature and humidity were similar to those already described. Special methods for different purposes will be given in the text under the description of the experiments concerned.

I. Resistance to unfavourable conditions

(a) *General*

The ability of this tick to survive unfavourable conditions is remarkable the absence of a suitable host, the adult has been found to survive witho meal for thirty-one months; nymphs and larvae were able to engorge a fasting thirteen and fifteen months respectively (MacLeod, 1932). Gib Carmichael (1884) stated that he had kept females under water from 2 t days, and that the ticks did not show any weakness on being removed. Ol (1927) records that larvae which hatched under water and remained submer survived for $1\frac{1}{2}$ months, and Totze (1933) says that larvae were unaffected submersion for 80 days. The writer kept females submerged for 21 days temperature of about 15° C. On being removed, they walked away appare unaffected.

(b) *Cold resistance*

Different unfed stages were placed in small vessels containing damp sand, and the vessels placed in a freezing chamber. The temperature of chamber was lowered a few degrees each successive day. Similarly, exposure for the required period, the ticks were gradually brought up thr daily increases of temperature to that of the laboratory, and there exam for death or survival. Table I gives the results of exposure of the three stag temperatures varying from 0° to −15° C. It will be seen that the tick i its stages can survive exposure for 4 days to a temperature of −8° C. killed by 1 day's exposure to a temperature of −15° C.

Table I. *Resistance to low temperatures.*

Commencing temperature ° C.	Reduced during (days)	Final temperature in ° C.	Exposed for (days)	Raised during (days)	Result
		Larvae			
16	1	0 to 3	45	1	Survived
	3	−5 to −4	3	—	,,
	5	−8 to −4	10	2	,,
	5	−7 to −5	6	2	Killed
	3	−8	4	—	Survived
	3	−12	3	2	,,
	7	−14 to −12	1	6	,,
	8	−12	2	4	Some survived
	7	−15	1	6	Killed
		Nymphs			
16	3	−5 to −4	3	—	Survived
	3	−8	4	—	,,
	3	−14 to −12	2	4	Killed
	8	−14 to −12	1	6	,,
	3	−12	3	2	Survived
	7	−15	1	6	Killed
		Females			
16	3	−5 to −4	3	—	Survived
	3	−8	4	—	,,
	3	−14 to −12	2	4	Killed
	8	−14 to −12	1	6	,,
	3	−12	3	2	Survived
	7	−15	1	6	Killed

Table II gives the comparative resistance to low temperatures of recently hatched and older larvae. It will be seen that larvae which have been hatched for some time are able to survive lower temperatures and for longer periods than larvae recently hatched.

(c) *Thermal death-point*

With increasingly high temperatures, the influence of humidity in prolonging the survival period of the exposed ticks steadily diminishes. Thus, nymphs at 35° C. survived 3–4 days at 70 per cent. saturation, 11–14 days at 100 per cent., and survived indefinitely at 90 per cent. At 37·5° C. they were killed at all humidities by 15 days' exposure, surviving less than 1 day at 70 per cent., and 6–9 days at 90 per cent. At 45° C. they were killed by exposure for 1 hour at 70, 90 and 100 per cent. Larvae exposed at 35° C. survived less than 1 day at 70 per cent., and were killed in 11–14 days at 90 per cent. and 100 per cent.; at 37·5° C. they were killed by exposure for 2 days at 90 per cent. and 6–9 days at 100 per cent. They were killed by 24 hours' exposure in saturated air at 40° C. and 22–54 min. exposure at 45° C.

Table II. *Resistance to low temperatures of older versus newly hatched larvae.*

Stage	Temperature ° C.	Duration of exposure (days)	Result
1–7 days	0	7	Survived
	−9 to −4	3	Killed
	−9 to −4	2	,,
7 weeks old	−11 to −9	5	Some survived
	−11 to −9	6	Killed

It would appear therefore that at 35° C. larvae are less resistant than nymphs at humidities below saturation, but equally resistant in saturated air. At 37·5° C. the same holds good, but the humidity range within which there is a differential resistance is much more limited. At 45° C. both stages were killed by 1 hour's exposure, regardless of humidity. Since the nymph is tracheate, and the larva non-tracheate, their differential resistance at humidities below saturation is probably related to the difference in their mechanisms for water exchange with the surrounding air. The temperature at which the difference in their survival periods is no longer apparent will therefore correspond with the thermal death-point, at which humidity ceases to exercise any effect on survival. This point would appear to lie, for the tick, in the neighbourhood of 40° C.

II. CLIMATIC LIMITS FOR SURVIVAL

The duration of survival of nymphs and larvae was tested at temperatures of 2, 10, 15, 20, 22·5, 25, 27·5, 30, 32·5, 35 and 37·5° C., and at humidities of 0, 10, 30, 50, 60, 70, 75, 80, 85, 90, 95 and 100 per cent., at each temperature. The combinations of temperature and humidity were obtained by the methods previously described, with the addition that 0 per cent. humidity was obtained by the use of anhydrous P_2O_5. The ticks were confined in test-tubes, the mouths

of which were covered with fine-mesh muslin, and these placed in the diffe
climate systems, which were then sealed. To avoid fluctuations of tempera
and humidity, they were examined only at periods of 1, 2, 5, 10 and 15 d
Results were noted either as "survived" or 100 per cent. death. About
larvae were used in each system; all of them originated from the same
cluster. Unfortunately, the number of available nymphs of the same age
limited, so only four were used at each climate combination. This was
pensated for, however, by the large number of records obtained, as a resu

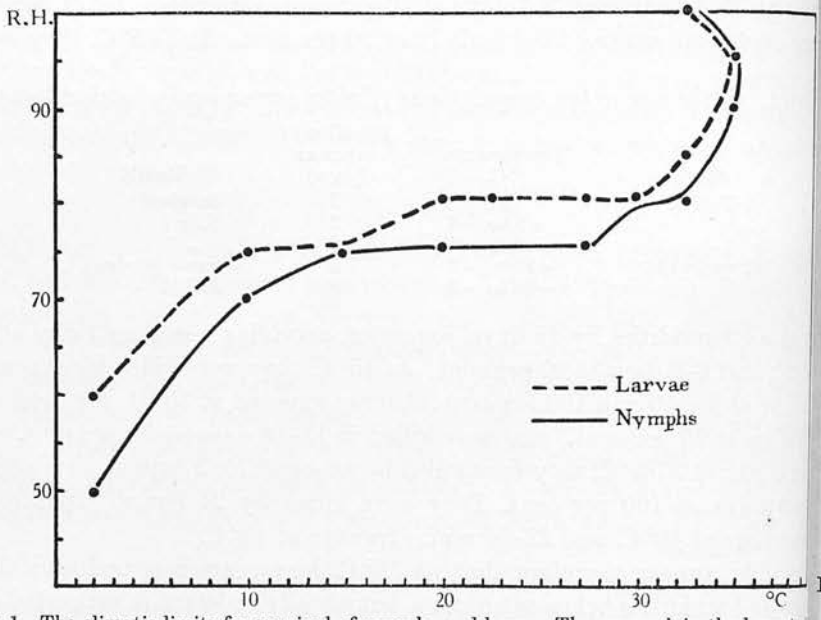

Fig. 1. The climatic limits for survival of nymphs and larvae. The curves join the lowest
humidity for each temperature at which any ticks survived for 15 days.

the extreme closeness of the intervals in both the temperature and hum
scales.

The experiment was discontinued after 15 days. Fig. 1 shows the limi
which some ticks were still alive after this time. The curves are obtaine
joining the points representing the lowest humidity for each temperatu
which survival occurred. These curves may be taken as indicating the app
mate limits of temperature and humidity at which the tick will survive.
again, as in the case of the limits for development of the gorged tick, the
striking feature is the narrow range of humidity within which survi
possible. Even at a temperature of 10° C., the lower humidity limit fo
vival of both stages lies between 70 and 75 per cent., while at temperatu
15–30° C. it lies between 75 and 80 per cent. It is to be remembered also
this limit represents that below which 100 per cent. death occurred in 15
so the limit for 100 per cent. or even 50 per cent. survival over a longer p
will be even higher.

These findings are in agreement with those of Olenev (1927), who, working with temperatures varying between 10 and 20° C., found that, at 70 per cent. R.H., 50 per cent. of the larvae were dead by the sixth day, 75 per cent. by the ninth and 100 per cent. on the tenth day.

The nymphs appear to be slightly more tolerant of dry conditions than the larvae, while, at the upper temperature limit of 35° C., both stages die in saturated air while surviving in air 95 per cent. saturated.

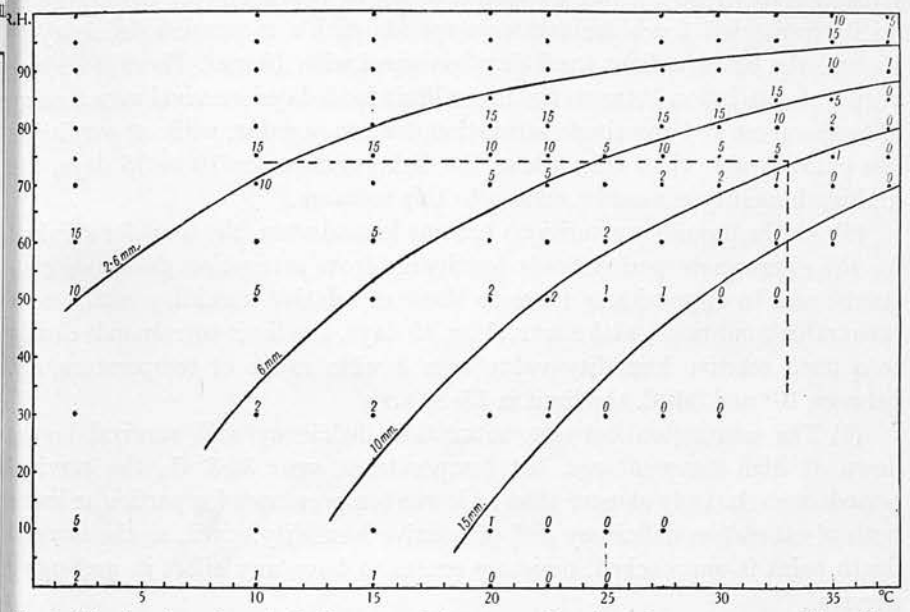

Fig. 2. The duration of survival of larvae at different combinations of temperature and humidity. The points indicate the combinations at which survival was tested. Only the lowest relative humidity at each temperature for survival for periods of 15, 10, 5, 2 and 1 day respectively have been indicated by the appropriate figure.

III. Influence of the humidity factor on duration of survival within the critical temperature limits

(a) *Comparative survival of nymphs and larvae*

If the survival periods of the tick are plotted on a chart, of which the ordinates are temperature and relative humidity, the intereffects of these factors on the duration of survival becomes clear. Figs. 2 and 3 represent the survival of larvae and nymphs respectively at different combinations of temperature and humidity. Where the ticks were killed in 1 day, the figure 0 is noted. If they survived 1 day, but were killed in 2 days, the figure 1 is entered, and so on. To simplify the figure, only the lowest humidity point for survival at each temperature is noted. The dots indicate the combinations at which survival was tested. Across the diagrams lines have been drawn corre-

sponding to certain fixed saturation deficiency values. Fig. 2 illustr
several points of interest.

(1) At unfavourable humidities, *i.e.* humidities of 70 per cent. or lo
larvae at any fixed relative humidity survive longer at low temperatures
at high.

(2) Within certain limits of temperature and humidity—marked on
diagram by interrupted lines—the duration of survival appears to be relate
saturation deficiency. Thus, at temperatures of below 30° C., the lower
midity limit for 1 day's survival corresponds with a saturation deficienc
15 mm. Hg, and the limit for 2 days' survival with 10 mm. There is a le
degree of correlation between the lower limit for 5 days' survival over a ra
of temperature and any single saturation deficiency value, while at condit
less unfavourable than this, where the tick survives for 10 or 15 days,
limiting humidity cannot be related to this measure.

(3) As the humidity conditions become less adverse, the limit for surv
for the appropriate period tends to diverge from saturation deficiency
stants, and to approximate more to those of relative humidity until, u
favourable conditions, with survival for 15 days, the limit corresponds clo
to a fixed relative humidity value over a wide range of temperature,
between 10° and 30° C. the limit is 75–80 R.H.

(4) The correlation between saturation deficiency and survival br
down at high temperatures. At temperatures over 32·5° C., the surv
periods are relatively shorter than at lower temperatures for particular li
both of saturation deficiency and of relative humidity, until, as the the
death point is approached, moisture ceases to have any effect in prolon
survival.

A study of Fig. 3 shows that, in the case of the nymph, survival u
highly unfavourable humidity conditions is not related to saturation deficie
at least at temperatures of over 25° C. Thus, at 32·5° C., the lower lim
saturation deficiency which the nymph can tolerate for 2 days is 15
deficiency, while at a temperature of 27·5° C. the nymph survives for
period at a deficiency of 25 mm. At intermediate conditions, there appea
be some correlation. Thus, the lower limiting humidity for 5 days' survi
fairly closely represented by a saturation deficiency of 10 mm. There
much lesser degree of correlation, and over a lesser temperature range, betw
saturation deficiency and the limiting conditions for 10 days' survival—
interrupted line indicates the approximate humidity limit—while there i
agreement between the limits for survival for 15 days and any satura
deficiency.

It is evident that the nymph is more tolerant of aridity than the la
that is, it would appear to possess some mechanism, absent in the larva,
which it can reduce the rate of loss of water under unfavourable mois
conditions. Since the larva is non-tracheate, loss of water in its case mus
from the general body surface. In the tracheate nymph, on the other h

loss of
pointed
drying
under a
It i
stages.
of the l
the gre
aridity
of arid

H.
90
80
70
60
50
40
30
20
10
15
10
5

Fig. 3.
mid

mecha
At the
two st
water
produc

It
heat in
tion of
lower t
at a fix
provid

Paras

loss of water is probably mainly from the tracheal tree. Buxton (1932) has pointed out that tracheate species of arthropods appear to be more resistant to drying than non-tracheate species. It is possible, therefore, that the nymph under arid conditions conserves moisture by closing the spiracles.

It is of interest to compare the humidity limits for survival of the two stages. In Fig. 4 the limits for 1 day's survival are compared; the comparison of the limits for 2 days' survival presents a similar picture. It will be seen that the greater toleration of the nymph becomes less marked at extremes both of aridity and temperature. The convergence of the limits at extreme conditions of aridity is of interest, and suggests a collapse of the water-conserving

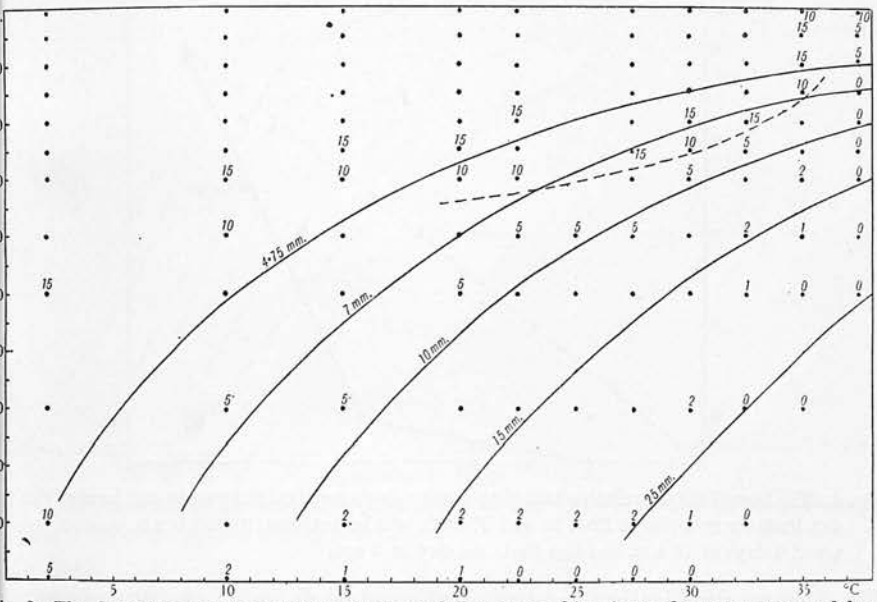

Fig. 3. The duration of survival of nymphs at different combinations of temperature and humidity.

mechanism, so that the nymph loses moisture almost as rapidly as the larva. At the temperature extreme, the difference between the toleration limits of the two stages decreases because the distinctive ability of the nymph to conserve water becomes of decreasing importance, aridity playing a decreasing part in producing death as the thermal death-point is approached.

(*b*) *Intereffects of temperature and humidity*

It has been shown that with increasing temperature the partial effect of heat in causing death increases. At higher temperatures, therefore, the duration of survival will not maintain the same relation to rate of water loss as at lower temperatures. If it be assumed that this harmful effect of heat requires, at a fixed temperature, a fixed time to operate, then even at one temperature, provided this is above the optimum, duration of survival will not be pro-

portional to rate of loss of water. Thus, the slower the rate of water loss greater proportion of the lethal effect is attributable to heat, death occurri such case before the maximum amount of water is lost which the organism tolerate. Therefore, even at one temperature, if this be above the optim duration of survival will not be exactly proportional to saturation deficie even although the rate of water loss be so. This hypothesis is supported by following experiment.

Six groups of twenty unfed nymphs were exposed at a temperatur 34° C. to humidities of 90, 70, 50, 30, 10 and 0 per cent. relative humi They were examined every few hours, and the number of deaths recor

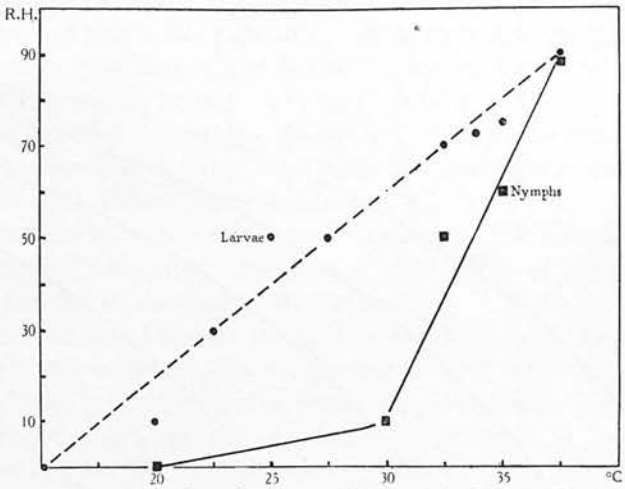

Fig. 4. The lower limiting relative humidity for one day's survival in nymphs and larvae. T day limit for nymphs at 22·5, 25 and 27·5° C. will lie between 10 and 0 R.H., since th vived 2 days at 10 R.H. and less than one day at 0 R.H.

Fig. 5 shows graphically the duration of survival at each humidity, percen mortality being plotted against time. From the figure, the time point f per cent. death at each humidity can be obtained.

If the time in hours required for 50 per cent. death is multiplied b saturation deficiency (S.D.) corresponding to each humidity, the follo series of values is obtained:

R.H.	Hours	×	S.D.	=	P
70	32	×	11·97	=	383
50	27	×	19·95	=	539
30	20	×	27·93	=	559
10	18	×	35·91	=	646
0	14	×	39·90	=	559

Now, if survival were inversely proportional to saturation deficiency, product of the two (P) should be a constant. In the above experiment P increasing value with decreasing humidities down to 10 per cent. That is tick survives relatively longer at low humidities than at high. This w indicate that with decreasing humidity death becomes due more and mo

loss of water, the heat-lethal effect having increasingly less time to operate, and, consequently, being responsible for an everlessening share in producing death. Therefore, as the cause of death becomes more and more due to loss of water, an increasing proportion of the water content in the body requires to be lost, until the maximum amount is reached which the tick could lose under any conditions, death being then due solely to water loss.

An interesting point is the unexpectedly low P value for 0 per cent. humidity. Here, again, there would appear to be a collapse of the water-conserving mechanism, so that water is lost at a relatively greater rate than at other humidities.

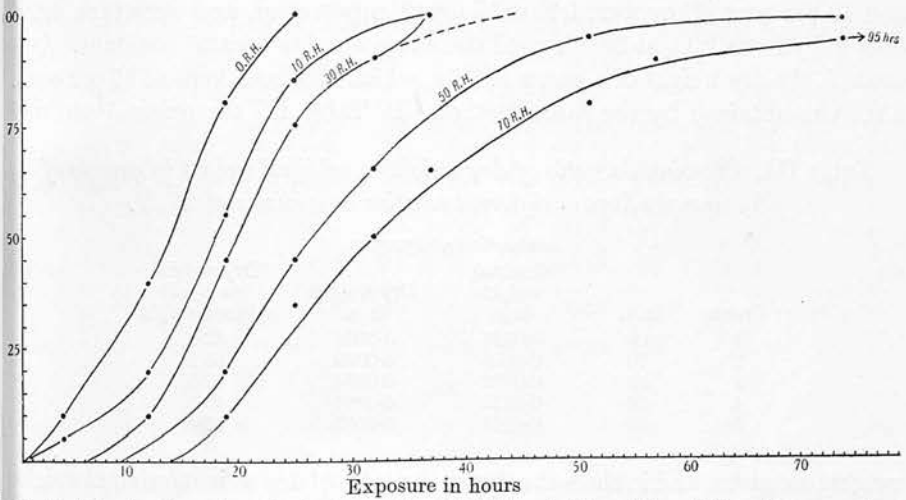

Fig. 5. The duration of survival of nymphs at 34° C. and different humidities. The percentage death is plotted against time in hours.

(c) *Relation of saturation deficiency to loss of water*

It has been shown that survival of the tick can be measured by saturation deficiency only under limited conditions both of temperature and humidity. The deviation at higher temperatures is due to the interference of the heat-lethal factor; there remains to consider the case of deviation at temperatures where this effect might be expected to be inoperative, and death be attributable entirely to loss of water. The question of water loss in insects has received considerable attention in recent years, and it was felt desirable to investigate the question in relation to the tick in some detail, more especially as the tick is peculiarly suited to this type of study. It can live in the unfed condition at room temperature for upwards of a year. Destruction of body tissues by metabolic processes must, therefore, be very slow: over a period of days the loss due to this cause must be almost inappreciable, and so experimental variations in body weight over such periods can justifiably be regarded as simple effects of external environmental causes. Further, under unfavourable moisture conditions, death can be shown to be due to loss of water from the

tissues. In *Tenebrio* and in *Rhodnius*, Buxton (1930 and 1932 *a*) has shown loss of water from the tissues is compensated by increased productio metabolic water, so that the ratio of dry weight to total weight remains stant. Death will, therefore, be due more to exhaustion of tissues tha simple water loss, and, therefore, because of gaseous interchange, the lo weight of the organism cannot strictly be regarded as being an exact reflec of the evaporation rate of free water from the body.

That this compensating activity does not take place in the case of the appears from the following experiment. Groups of approximately fifty u nymphs each were weighed and exposed at 25° C. and humidities of 70, 5 and 10 per cent. They were left until death supervened, and were then d over anhydrous P_2O_5 at 50° C. until their dry weights became constant. control, the dry weight of a group of fifty, which had been kept at 90 per c R.H., was obtained by the same method. In Table III the original and

Table III. *Showing the ratio of dry weight to original weight in groups fifty nymphs kept at different relative humidities at* 25° *C.*

Ixodes ricinus nymphs

Group	R.H.	Original weight in g.	Dry weight in g.	Dry weight as % of original weight
1	90	0·0121	0·0064	52·9
2	70	0·0105	0·0059	56·2
3	50	0·0122	0·0064	52·5
4	30	0·0132	0·0065	49·3
5	10	0·0121	0·0067	55·4

weights are given, and in the last column the ratio of dry weight/original w is given. It will be seen that the ratio is practically constant for all humidi Therefore, since the nymphs at the lower humidities lost weight before d the ratio of dry weight to total weight at death must have been different to obtaining at 90 per cent., where there is no appreciable loss of weight of fas ticks over a period of days. In other words, loss of water in the tick is compensated by increased destruction of tissue to produce metabolic wa and loss of weight is therefore a direct indication of the rate of evaporatio water from the body.

The method adopted in this and the subsequent weighing experiments as follows. Small metal capsules were prepared, open at one end and ha the other end closed with fine-mesh wire gauze. The ticks were placed in t and the open end closed with lead foil, held in place by a thin rubber ba The containers were then weighed, an analytical balance being used, w weighed to 10^{-4} g. Since the average weight of a nymph is approxima 2×10^{-4} g., it was necessary, in order to get significant results, to weigh gro of fifty or more. Each container was suspended by a looped string inside appropriate humidity system and weighed daily. At the end of the experim the containers minus the ticks were weighed, and the weights of the t calculated. Since the container consisted entirely of metal, with the excep

of the thin ru
organic mater
gauze been us
Groups of
different hum
later, it is nec
sequently, the
Three experim
daily losses in
weight loss h

Table IV.

Group	Original weight g.
1	0·0105
2	0·0112
3	0·0099
Total	0·0316
1	0·0122
2	0·0103
3	0·0109
Total	0·0334
1	0·0132
2	0·0097
3	0·0107
Total	0·0336
1	0·0121
2	0·0110
3	0·0108
Total	0·0339

* The we

Each unit wa
will be seen th
weight had be
At 70 per
pected interru
to an actual
occurred. The
possibility of
significance of
If the rate
product of th
humidity sho
from the total
deficiency. It
water is relate
humidities agr
the relation b
day, on which
the calculation

of the thin rubber band, there was no variable introduced by hygroscopy of organic material, as would have been the case had cotton-wool plugs or muslin gauze been used.

Groups of nymphs of the same previous history were exposed to 25° C. and different humidities. This temperature was chosen because, as will be shown later, it is near the optimum temperature range for the unfed tick and, consequently, the heat-lethal effect may reasonably be expected to be very slight. Three experiments were carried out, at different times, and Table IV shows the daily losses in weight at the different humidities in each experiment. Each weight loss has also been expressed as a percentage of the original weight.

Table IV. *Daily loss of weight of nymphs at 25° C. and several humidities.*

	Original weight	Day 1		Day 2		Day 3		Day 4		Day 5		Day 6		Total weight loss %
Group	g.	g.	%	g.	%	g.	%	g.	%	g.	%	g.	%	
1	0·0105	0·0010	9·5	0·0008*	7·6	0·0009	8·6	0·0009	8·6	0·0008	7·6	—	—	30·5
2	0·0112	0·0014	12·5	0·0001	0·9	0·0004	3·6	0·0005	4·5	0·0007	6·3	0·0008	7·1	34·9
3	0·0099	0·0013	13·1	0·0006*	4·0	0·0008	8·1	0·0006	6·1	0·0006	6·1	—	—	33·4
Total	0·0316	0·0037	11·7	0·0013*	4·1	0·0021	6·6	0·0020	6·3	0·0021	6·6	0·0008	7·1	—
1	0·0122	0·0010	8·2	0·0011	9·0	0·0011	9·0	0·0008	6·5	—	—	—	—	32·7
2	0·0103	0·0013	12·6	0·0003	3·0	0·0009	8·7	0·0006	5·8	—	—	—	—	30·1
3	0·0109	0·0009	8·3	0·0003	2·8	0·0006	5·5	0·0005	4·6	0·0007	6·4	—	—	27·6
Total	0·0334	0·0032	9·6	0·0017	5·1	0·0026	7·8	0·0019	5·7	0·0007	6·4	—	—	—
1	0·0132	0·0016	12·1	0·0014	10·0	0·0016	12·1	—	—	—	—	—	—	34·8
2	0·0097	0·0011	11·3	0·0010	10·3	0·0011	11·3	0·0010	10·3	—	—	—	—	42·9
3	0·0107	0·0015	14·0	0·0015	14·0	0·0012	11·2	—	—	—	—	—	—	39·2
Total	0·0336	0·0042	12·5	0·0039	11·6	0·0039	11·6	0·0010	10·3	—	—	—	—	—
1	0·0121	0·0022	18·1	0·0021	17·3	—	—	—	—	—	—	—	—	35·4
2	0·0110	0·0017	15·5	0·0016	14·5	0·0015	13·6	—	—	—	—	—	—	43·6
3	0·0108	0·0022	20·4	0·0012	11·1	—	—	—	—	—	—	—	—	31·5
Total	0·0339	0·0061	18·0	0·0049	14·5	0·0015	13·6	—	—	—	—	—	—	32·5

* The weights marked with an asterisk are increments over the previous day's weight.

Each unit was discontinued when over 50 per cent. of the ticks had died. It will be seen that death occurred when approximately one-third of the original weight had been lost.

At 70 per cent. relative humidity there was in each experiment an unexpected interruption of weight loss on the second day, in two cases amounting to an actual increment. Thereafter, weight was lost steadily until death occurred. The regularity of this result over the three experiments precludes the possibility of its being due to an error in weighing (see Fig. 6). The possible significance of this observation will be discussed later.

If the rate of loss of water is proportional to saturation deficiency, the product of the percentage loss and the reciprocal of the deficiency for each humidity should be a constant (K). In Table V the daily losses, calculated from the total of the three experiments, have been divided by the saturation deficiency. It appears that for humidities of 50 per cent. and less, rate of loss of water is related to this humidity measure, the K values at the different relative humidities agreeing within the limits 0·43–0·84. At 70 per cent. R.H., however, the relation breaks down, the K value ranging from 0·89 to 1·65. (The second day, on which the interruption of weight loss occurred, has been omitted from the calculation.) It would appear from the high value for K at 70 R.H. that the

nymph loses relatively more water into air 70 per cent. saturated than drier air. A similar finding has been recorded by Buxton (1930) for the worm, and by Mellanby (1932) for the bed-bug.

To test whether the relation under adverse moisture conditions held range of temperatures, a group of seventy-five nymphs was exposed to 2 and 30 R.H., and the daily weight loss calculated. The original weight o group was 0·0142 g. The daily loss in grammes, the percentage of the ori weight lost and the K value were as follows:

Day	g.	%	K
1	0·0016	11·27	0·92
2	0·0015	10·59	0·86
3	0·0010	7·04	0·57
4	0·0010	7·04	0·57

These values for K are in fairly close agreement with the values obtain 25° C. (0·43–0·84); that is, under highly unfavourable conditions of humi rate of loss of water is approximately proportional to saturation deficie both at different saturation deficiencies for one temperature, and at diff temperatures.

Table V. *Showing the ratio of weight loss to saturation deficiency for nymphs at 25° C. and several humidities.*

R.H.	70	50	30	10
Day 1	1·65	0·81	0·75	0·84
2	—	0·43	0·70	0·68
3	0·93	0·66	0·70	—
4	0·89	0·48	—	—
5	0·93	—	—	—
6	1·00	—	—	—

Since in two different types of experiment the survival of nymphs had found to be unexpectedly short in completely dry air (Figs. 4, 5), the ra water loss under such conditions was examined. A group of seventy nymphs, weighing 0·016 g., was exposed over anhydrous phosphorus pento at 20° C. Since, even at this temperature, 100 per cent. deaths occur in 2 (Fig. 3), only 1 day's weight loss could be obtained. The loss was 0·0051 g. 31·7 per cent. of the original weight. This divided by the saturation defici (17·54 mm.) gives a K value of 1·8. Thus, here again, we have evidence under completely dry conditions nymphs lose water at a relatively greater than at higher humidities. A tentative explanation of this has been adva earlier, viz. that under such extremely adverse conditions the nymph is un to close its spiracles.

Table VI shows the rate of loss of water of larval clusters at 25° C. different humidities. In this case also, loss of water appears to be roughly portional to saturation deficiency at the lower humidities—$K = 0{\cdot}80$–$1{\cdot}09$– the proportion breaks down at 70 per cent., K ranging from 0·68 to 1·82. experiment is, however, extremely rough, since the larva is so small clusters were used, and the end-point had to be determined arbitrarily,

once the conta
both extremel
seize without
Although l
water at rates
actually a gre
humidity than
possesses some
the rate of los
The possess
results obtaine
interest to com
temperatures.

Table VI

H.
D.

ay	Weight of larvae	Loss weigh per da
0	0·0210	—
1	0·0200	0·001
2	0·0173	0·002
3	0·0153	0·002
4	0·0128	0·002
5	Dead	—
6	—	—
7	—	—

interruption o
numbers indic
joining the cir
humidity of 7
first, decreases
effort at comp
while at 30° C.
water proceeds
irregularities n
some method
interruption of
larvae. No ex
logical principl
In this con
larvae, in so fa
into damp air

Buxton (19
of water and

once the container was opened, the larvae could not be enclosed again, being both extremely active and, also, on account of their minute size, difficult to seize without injury.

Although both the larvae and nymphs at certain humidities appear to lose water at rates proportional to the saturation deficiency, yet the larva loses actually a greater proportion of its water content per day at a particular humidity than the nymph. This further supports the hypothesis that the nymph possesses some mechanism whereby, under unfavourable moisture conditions, the rate of loss of water is reduced.

The possession of such a mechanism may be associated with the unexpected results obtained with nymphs at humidities only slightly unfavourable. It is of interest to compare the rate of water loss at 70 per cent. saturation and different temperatures. Fig. 6 illustrates the rates of loss at 20, 25 and 30° C. The

Table VI. *Loss of weight of larvae at 25° C. and several humidities.*

	70 7·1				50 11·9				30 16·6			
Day	Weight of larvae	Loss of weight per day	% of original weight	*K*	Weight of larvae	Loss of weight per day	% of original weight	*K*	Weight of larvae	Loss of weight per day	% of original weight	*K*
0	0·0210	—	—	—	0·0222	—	—	—	0·0210	—	—	—
1	0·0200	0·0010	4·8	0·68	0·0201	0·0021	9·5	0·80	0·0172	0·0038	18·1	1·09
2	0·0173	0·0027	12·9	1·82	0·0185	0·0026	11·2	0·94	0·0141	0·0031	14·8	0·89
3	0·0153	0·0020	9·5	1·34	—	—	—	—	Dead	—	—	—
4	0·0128	0·0025	11·9	1·68	Dead	—	—	—	—	—	—	—
5	Dead	—	—	—	—	—	—	—	—	—	—	—
6	—	—	—	—	—	—	—	—	—	—	—	—
7	—	—	—	—	—	—	—	—	—	—	—	—

interruption of weight loss at 25° C. has already been commented on. The numbers indicate the individual results of the three experiments; the curve joining the circles is based on the average loss per day. At 20° C. a relative humidity of 70 is only very slightly unfavourable; the rate of loss, rapid at first, decreases later. At 25° C. there would appear to be an early abortive effort at compensating for evaporation, after which, loss proceeds steadily, while at 30° C., at which temperature 70 R.H. is distinctly unfavourable, loss of water proceeds evenly right from the commencement. As has been said, the irregularities may possibly be connected with the possession by the nymph of some method of conserving water. Thus, there would appear to be no interruption of loss at 25° C. and 70 per cent. in the case of the non-tracheate larvae. No explanation can, however, be offered at present of the physiological principles underlying the phenomena.

In this connection it is of interest to note that the rate of water loss in the larvae, in so far as the results can be relied on, is greater, relatively speaking, into damp air than into dry, yet the larva has no tracheal system.

(*d*) *Saturation deficiency, loss of water and survival*

Buxton (1931, 1932) has collected a mass of evidence dealing both with loss of water and with survival, and has shown that, with certain limitations,

saturation deficiency governs the loss of water of fasting insects of se
species. Although recognising that exceptions exist, he suggests that
applies to the majority of insects. It has been shown above that this rela
ship applies also to the arachnid, *Ixodes ricinus*. It is of interest to consi
what extent Buxton's generalisation applies to survival. It has been seen
the relation of saturation deficiency to water loss at one temperature b
down both under conditions of extreme aridity and under conditions
slightly unfavourable, so, therefore, its relation to survival also must be su

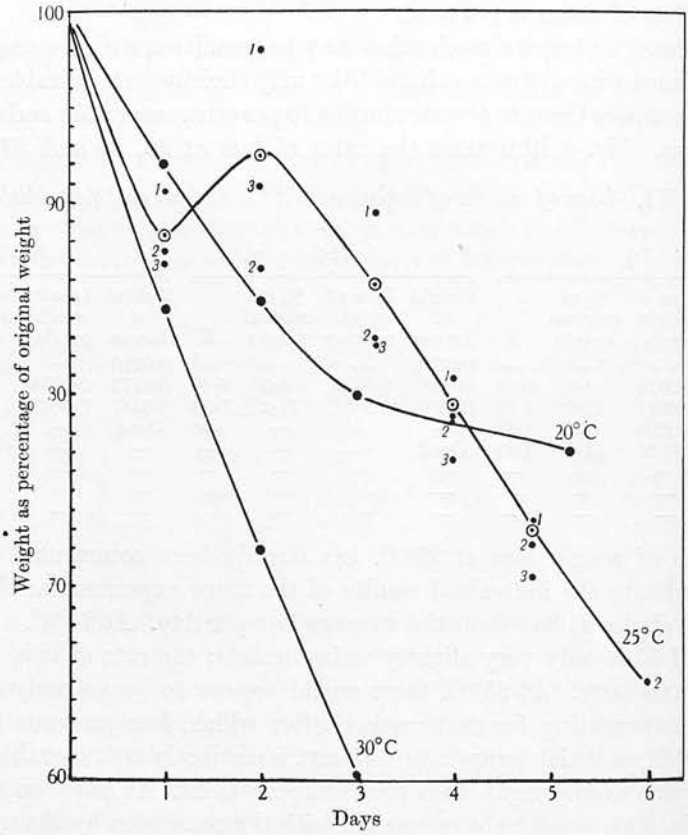

Fig. 6. The curves of percentage loss of weight of nymphs at 70 R.H. and different tempe
The curve for 25° C. is based on the average of three experiments; the individual res
indicated by numbers.

to these limits. Even within these limits, the duration of survival doe
maintain a fixed relation to rate of water loss, so the application of the rel
ship to survival must be further limited. Thus, at temperatures ove
optimum, there is an increasing heat-lethal effect with increasing tempera
As has been shown above, there is also at such temperatures an incre
heat-lethal effect with increasing humidity. It follows, therefore, that Bux
generalisation applies to survival of the tick only within strictly limited
ditions both of humidity and temperature. Since humidities only slightly

favourable ar
in so far as t
ditions in the
humidity for
over a narrow
suitability of
distribution o

In the pre
survival of th
conditions be
which condit
activity, and
by affecting t
It is clear
survival limit
humidity field
the narrow li
responses, but
the water cont
tick activity
apparent relat

Several ny
of which was l
a strip of pap
movement of t
the temperatu
noted.
Irregular
activity. Mov
and not until
was raised. WI
general in bot
began, marked
slowing down
heat stupor w
Raising the te
movement of
seconds per u
second—is rou
related to temp

favourable are without these limits, the practical utility of this generalisation in so far as the tick is concerned is very much reduced. Thus, since at conditions in the neighbourhood of the biological limit for the tick the limiting humidity for survival is not expressed by a single saturation deficiency, even over a narrow range of temperature, the law cannot be used in assessing the suitability of different climates or seasons, or in mapping the geographical distribution of the species.

IV. Influence of temperature on activity

In the preceding sections the limits of climatic conditions for indefinite survival of the unfed tick have been defined, and the duration of survival at conditions beyond these limits discussed. It is now necessary to consider which conditions, within this survival range, constitute the optimum for activity, and which, if any, produce responses conducive to host parasitisation, by affecting the relative accessibility of parasite and host.

It is clear that temperature is the important variable to be considered. The survival limits embrace a wide range of temperature and only a narrow humidity field. Further, changes in the moisture equilibrium of the air, within the narrow limits permissible, would not be expected to produce immediate responses, but rather to take effect through their prolonged application altering the water content of the body. It has already been shown (MacLeod, 1932) that tick activity can be correlated with air temperature, whereas there is no apparent relation between activity and rainfall.

(*a*) *Rate of activity*

Several nymphs and adults were placed in a corked tube, the atmosphere of which was kept saturated by a moist cotton-wool plug. Within the tube was a strip of paper marked in tenths of an inch, so that a measure of the rate of movement of the ticks could be obtained. The tube was placed in a water-bath, the temperature of which was steadily raised, and the behaviour of the ticks noted.

Irregular results were obtained with the lower temperature limit for activity. Movement in one or both stages began at 11° C. in some experiments, and not until 14° C. in others, according to the rate at which the temperature was raised. When the temperature was raised fairly rapidly, movement became general in both stages at 13° C. At 40° C. the stage of excited movement began, marked excitement being exhibited at 45° C. At 47° C. there was a slowing down of activity, and many of the adults became comatose. At 49° C. heat stupor was general in both stages, but recovery took place on cooling. Raising the temperature to 51° C. resulted in death. In Fig. 7 the rate of movement of nymphs at different temperatures is plotted, on a basis of seconds per unit (one-tenth of an inch). The reciprocal curve—units per second—is roughly sigmoid, suggesting that the velocity of movement may be related to temperature according to van't Hoff's formula for chemical reactions,

$Q_{10} = \frac{K_1}{K_0}\left(\frac{10}{T_1 - T_0}\right)$, if K be taken as the time required to travel a fixed nu ce, while the
of units. ange of tempe

(b) Preferred temperature y altering the

A careful and detailed study of the response of this tick to different late by a pap
peratures has been made by Totze (1933), who found that the pref luced, so ultim
temperature depended on the previous conditions of temperature to whic aseline impreg
void. The enc

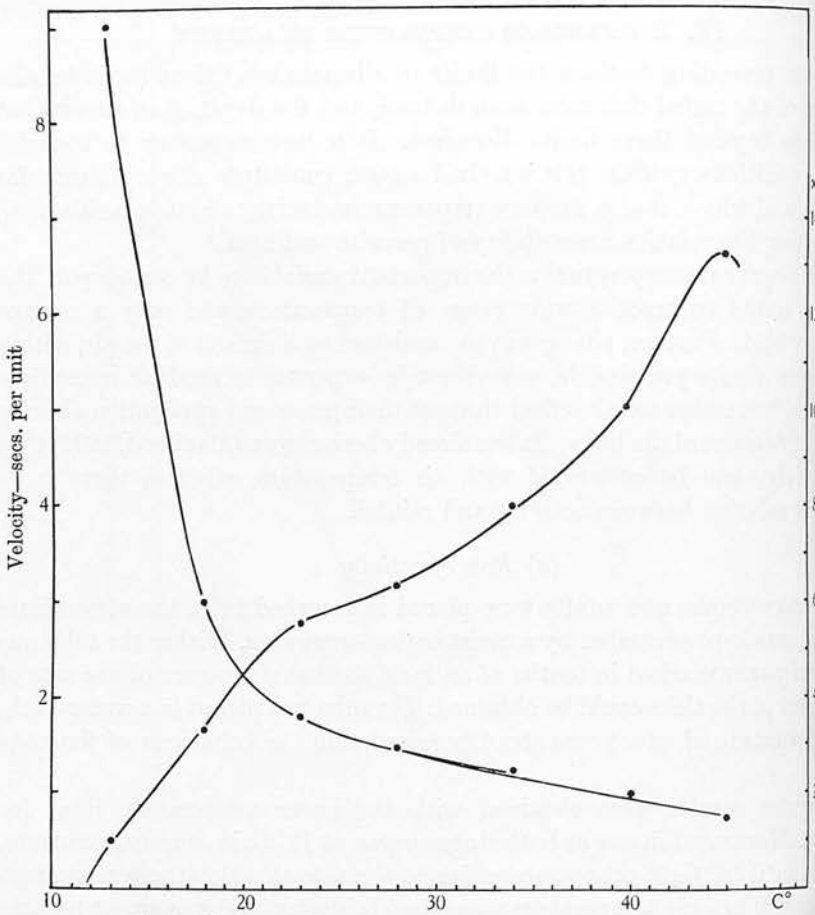

Fig. 7. The rate of movement of nymphs at different temperatures.

ures of which
f water was
nometer was

T
Temp. ° C
Exp.
Aver

emperature o
venly along th
The apparatus
were left on th
was taken. Ta
Those in the c
nained motion
perature prefe
inding of 17° C
arvae, the pref
espectively. T
From these
perature range

V. The

The evidenc
Thus, Hindle a
phototropic in
emale of *Mar*
eliotropic resp
Totze (1933) re
fully his metho
positively phot
nd below whi
been entirely u

ticks had been exposed, varying from 15° C., in the case of ticks previ maintained at 10–12° C., to 19° C. (nymphs and larvae) and 23° C. (ad when the previous temperature was 18–20° C. He found that ticks co adapted to different preferenda by subjecting them for 2–2·5 hours to hig lower preliminary temperatures.

In the experiments described below, the ticks used had been bred at temperature (14–18° C.). The method adopted was as follows:

A copper strip, 30 × 3 in., was placed so that one end supported a bl

ce, while the other was warmed by a bunsen jet below it. There was thus a ange of temperature along the copper strip, the limits of which could be varied y altering the size of the jet. It was found that if the ticks were confined to the late by a paper flange, the complicating factor of thigmotropism was introduced, so ultimately the method adopted was to border the plate with a strip of aseline impregnated with clove oil, contact with which ticks had been found to void. The enclosed area of the plate was marked off into sections, the temperatures of which were first obtained for each experiment as follows. A small pool f water was placed on each section. After half an hour the bulb of a thermometer was placed in the water, and an approximate index of the surface

Table VII. *Preferred temperature for unfed nymphs.*

Temp. ° C. ...	7–10	11–13	14–17	18–21	22–25	26–30
			No. of ticks in each section			
Exp. I	10	4	13	3	1	1
II	5	0	20	2	4	5
III	13	3	22	5	0	0
IV	17	9	28	3	5	0
Average	11	4	21	3–4	2–3	1–2

emperature of the section was thus obtained. The ticks were distributed evenly along the plate, and left to choose whichever section was most suitable. The apparatus was roofed over with black cloth to exclude light. The ticks were left on the plate for about 1 hour, and then the result of the experiment was taken. Table VII records the results of the experiments with nymphs. Those in the coldest section were probably inactivated by the cold and remained motionless. If this section be ignored, it would appear that the temperature preferred by the nymphs was 14–17° C. This agrees with Totze's finding of 17° C. for nymphs reared at 14–18° C. In two similar experiments with larvae, the preferred temperature range was found to be 16–17 and 18–21° C. respectively. Totze records the larvae as behaving similarly to the nymphs.

From these and Totze's results, one may assume that the preferred temperature range of the tick lies between the limits of 14 and 23° C.

V. THE PHOTOTROPIC RESPONSE AT DIFFERENT TEMPERATURES AND HUMIDITIES

The evidence with regard to phototropism of ticks in general is conflicting. Thus, Hindle and Merriman (1912) found that *Argas persicus* was negatively phototropic in all stages. Similarly, Hunter and Hooker (1907) record that the female of *Margaropus annulatus*, an eyed tick, is strongly negative in its heliotropic response. Yet, in the eyeless *Ixodes ricinus*, Olenev (1927) and Totze (1933) record a positive phototropism for the unfed tick. Totze describes fully his methods and results, which indicate that all the unfed stages are positively phototropic, and that there is an optimum intensity of light above and below which the ticks are less marked in their response. The writer has been entirely unable to confirm this result.

The response of the tick to light was tested in three different ways:

(1) A sheet of white paper was placed on a hot plate, the temperature of which electrically controlled. This was placed near a window, ticks liberated on to it, and their traced. In all instances they were negatively heliotropic.

(2) Ticks were distributed evenly inside long glass test-tubes, which were pla different positions on a copper plate. This was supported on trestles, with a row of g under one end. There was thus a temperature gradient along the plate, the limits of could be adjusted by altering the flame of the jets. This method prevented any movement, and gave a similar result to the first method.

Following on this work, a routine method of manipulation of ticks pending on their negative phototaxis, has been successfully used for th few years.

Subsequently to the above work, Totze's work was published, and, sin results were in direct contradiction to the writer's findings, a careful stu the subject was made, under properly controlled conditions of temper humidity, and radiant heat.

(3) A water-jacketed thermal cabinet was used for controlling temperature; di degrees of humidity were obtained by the use of potash solutions. A solution of the re concentration was placed in a large petri dish, over which was then stretched a piece muslin gauze, held taut by a rubber band. On this the ticks were placed. Another gla of the same diameter was inverted over the first, and thus the ticks were enclosed in space, the relative humidity of which depended on the concentration of the solution be The whole was placed in the cabinet, the temperature of which had been brought required degree, and left for an hour, so that the temperature and humidity in the might attain to equilibrium. Light from a 60 watt lamp, 1 ft. away, was then ad through a glass pane in one side of the cabinet, and the reaction of the ticks observed th a sliding panel in the roof of the cabinet. The light, before entering the cabinet, was through a bath of 1 per cent. ferric sulphate solution, which absorbed the heat rays.

In all the experiments, it was observed that the ticks exhibited definite response than a general tendency. Thus, some individuals rem indifferent for some time, wandering at right angles to the light rays; travelled towards the light source for some distance; but all eventually t to congregate at the side of the vessel farthest away from the light.

Both adults and nymphs were tested, and experiments were carried each of the following temperatures and humidities, the result being in all the same—a negative phototropic response.

Temperature ° C.	R.H.				
11	100	90	—	—	—
14	100	—	—	—	—
16	100	90	70	50	—
17	100	90	—	—	—
22	100	—	70	—	—
25	100	90	70	50	—
28	100	90	70	50	30
30	—	—	70	—	30
33	—	—	70	50	30
35	100	90	70	50	30
38	—	90	70	50	—
40	100	—	70	50	30

In Totze's experiments also, radiant heat was absorbed by a suitable solution, so the difference in the results cannot be due to positive thermotaxis introducing a source of error, and therefore remains unexplained.

Gorged nymphs and larvae were also found to be negative in their reaction.

VI. THE INFLUENCE OF TEMPERATURE ON GEOTROPIC RESPONSE

The following method was used for studying the reaction of the tick to the stimulus of gravity at different degrees of temperature. A glass cylinder of in. diameter was placed upright in a copper water-bath, so that it projected about 9 in. above the level of the bath. This and the bath were filled with water, the temperature of which could be kept at any desired degree by the regulating mechanism of the bath. A number of special tubes were prepared by removing the flanges from test-tubes and holding each couple together, mouth to mouth, by a strong, narrow rubber band. Each tube was thus domed at both ends, and this eliminated the possibility of complicating modifications from thigmotropic stimuli. One end of each containing tube was ground down until the glass was perforated. Over the hole a piece of muslin gauze was pasted. The continuity of the inner surface of the tube was thus maintained, while the muslin allowed of the humidity in the tube being regulated.

By placing one of these tubes, containing ticks, in the exposed part of the glass cylinder, it was possible to expose the ticks to any desired temperature in daylight. A weight attached to the lower end of the tube kept it practically submerged in the water, the perforated end only being above the surface. The narrow diameter of the cylinder prevented the tube from leaving the upright position. Similarly, to expose ticks in darkness to any desired temperature, the containing tube was placed inside the copper water-bath with an attached weight to keep it upright, and submerged except for the perforated end.

Fig. 8 shows the geotropic response of unfed larvae at different temperatures, with and without the presence of daylight. A closed circle indicates a marked tendency, involving all, or the great majority of, the larvae; an open circle indicates a less definite but appreciable tendency. Circles on the left of the vertical lines indicate a positive geotropic response; on the right, a negative response. A limited number of experiments with unfed nymphs suggests that the response of this stage is similar to that of larvae.

It will be seen from the figure that, in darkness, larval ticks are positively geotropic at temperatures below 12 and above 30° C. At temperatures between these limits they are negatively geotropic. Under the influence of daylight the intensity of response is greater, and the range of temperature for which the tick is negatively geotropic is more clearly defined as 14–24° C.

It has been shown previously that ticks are inactive at temperatures below 10° C. From the above result it might be assumed that at temperatures of 10–14° C., although active to a greater or lesser extent, they tend in nature to remain at the roots of vegetation. Again, at temperatures of over 24° C., the ticks would be expected to forsake the vegetation for the surface of the ground.

A similar inhibiting effect of high temperatures on negative geotropism has been found by Fraenkel (cited by Uvarov, 1931) in the case of the desert locust, the hoppers of which climb the plants only at temperatures below 30° C., while above it they remain on the ground.

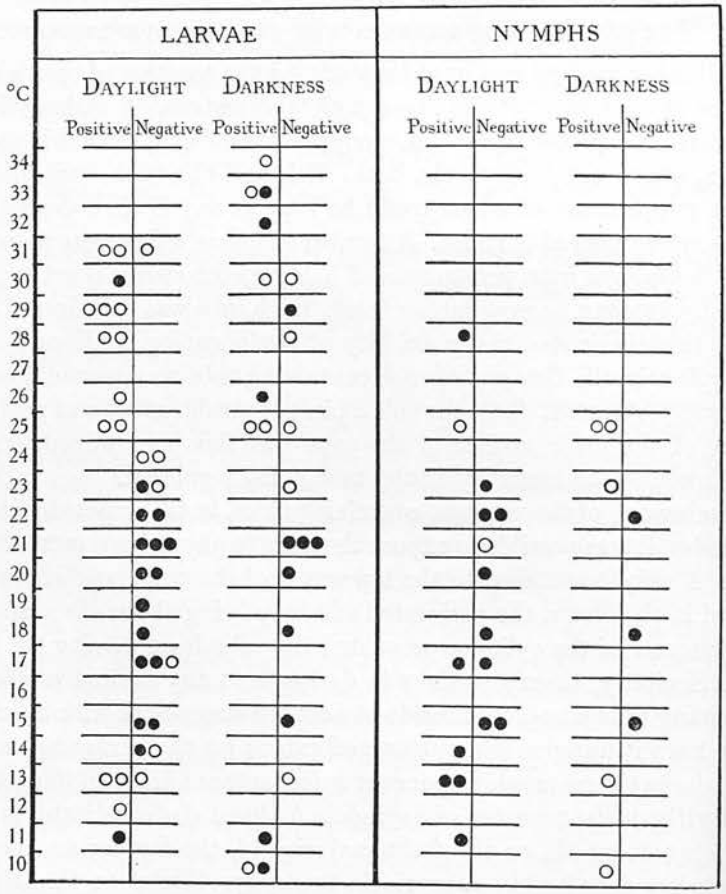

Fig. 8. The geotropic response of larvae and nymphs at different temperatures. Closed circles indicate a definite response; open circles a less definite but appreciable response. Circles to the left of the vertical lines indicate a positive, and on the right, a negative response.

VII. Discussion

The most marked feature of the climatic requirements for survival of unfed *Ixodes ricinus* is the high degree of humidity necessary. Saturated air appears to have no adverse effect on vitality, a markedly different result from that obtained by Cunliffe (1921, 1922) for *Ornithodorus moubata* and *savigni* ticks of dry climates, which are adversely affected by excess moisture. The lower limit of humidity for survival of *Ixodes ricinus*, throughout the limits of temperature normally obtaining in nature in this country, is fairly closely represented by a relative humidity value between 70 and 80.

The tick shows considerable powers of resistance to freezing, if the temperature be lowered slowly so as to allow of the development of a cold hardiness; the upper temperature limit for survival, on the other hand, is not very high.

Within these survival limits of temperature and humidity, the conditions necessary to allow of the tick's gaining access to hosts are those which permit of normal activity. It has been shown that the tick becomes active at temperatures of 11° C. and over. If the preferendum temperature be taken as the most favourable for normal activities, the limits of 14–23° C. are indicated.

In Nature, the unfed tick is found on the tops of vegetation, whence it is rubbed off by passing hosts. The second condition, therefore, under which access to hosts is favoured is that which induces a climbing habit. The tick is negatively geotropic in daylight within the temperature limits of 14–24° C. Within this range they will tend to congregate on tops of grass, rushes and shrubs. The limiting factor for host parasitisation, as opposed to that for survival, would therefore appear to be primarily temperature, opportunities for attachment to a host being most favourable at temperatures of 14–24° C.

The various experiments with unfed ticks have been carried out at all seasons of the year, as have also the processes of feeding and development. In no case has any indication been obtained of the overwintering torpor of unfed ticks described by Totze (1933), or of gorged ticks, Falke (1931). Falke's hypothesis has been discussed in my previous paper. Totze mentions a recognisable dullness as the sign of approaching torpor, which lasts from mid-September to the beginning of April, and which is not affected by altering the temperature or humidity. This could be possible only if there occurred in the tick an auto-intoxication from development, necessitating a seasonal diapause for physiological purification, comparable to the asthenobiosis of heterodynamic insects (Roubaud, 1922). The fact that ticks have been fed, and the gorged stages hastened through development at favourable temperatures in winter and summer, with no difference in the time required for metamorphosis (MacLeod, 1934), is sufficient evidence that in this country, at any rate, such seasonal variation in metabolic activity does not exist.

REFERENCES

BUXTON, P. A. (1930). *Proc. roy. Soc.* B, **106**, 560.

—— (1931). *Proc. R. ent. Soc. Lond.* **6**, 27.

—— (1932). *Biol. Rev.* **7**, 275.

—— (1932*a*). *Parasitology*, **24**, 429.

CUNLIFFE, N. (1921). *Ibid.* **13**, 327.

—— (1922). *Ibid.* **14**, 17.

FALKE, H. (1931). *Z. Morph. Ökol. Tiere*, **21**, 567.

GIBSON-CARMICHAEL, T. D. (1884). Note appended to Third Report, Special Committee to investigate Loupingill. *Trans. H. and A. Soc.* **16**, 301.

HINDLE, E. and MERRIMAN, G. (1912). *Parasitology*, **5**, 203.

HUNTER, W. D. and HOOKER, W. A. (1907). *Bull. U.S. Bur. Ent.* No. 72.

MacLeod, J. (1932). *Parasitology*, **24**, 382.
—— (1934). *Ibid.* **26**, 282.
Mellanby, K. (1932). *Ibid.* **24**, 419.
Olenev, N. O. (1927). *Défense des Plantes*, **4**, 354.
Roubaud, E. (1922). *C.R. Acad. Sci.*, Paris, **174**, 964.
Totze, R. (1933). *Z. vergl. Physiol.* **19**, 110.
Uvarov, B. P. (1931). *Trans. R. ent. Soc. Lond.* **79**, 1.

(*MS. received for publication* 23. vi. 1934.—Ed.)

PARASITOLOGY is published about four times a year. The numbers afterwards are issued in volumes each containing four numbers.

Papers for publication should be sent to Professor D. KEILIN, Sc.D., F.R.S., Molteno Institute, Downing Street, Cambridge. Other communications should be addressed to the University Press, Cambridge.

Papers forwarded to the Editors for publication are understood to be offered to *PARASITOLOGY* alone, unless the contrary is stated.

Contributors receive twenty-five copies of their papers free. Additional copies, not exceeding 100 (except in special cases), may be had at cost price: these should be ordered when the final proof is returned.

The subscription price is £2. 15*s*. per volume (post-free), payable in advance; single numbers 18*s*. 6*d*. net (double number 37*s*. net). Subscriptions may be sent to any Bookseller, or to The Cambridge University Press, Fetter Lane, London, E.C. 4.

The Cambridge University Press has appointed the University of Chicago Press agent for the sale of *Parasitology* in the United States of America.

This paper has been accepted for publication in "Parasitology". JMcL.

IXODES RICINUS IN RELATION TO ITS PHYSICAL ENVIRONMENT

III. CLIMATE AND REPRODUCTION

by

John MacLeod,
Carnegie Research Fellow,
Moredun Institute,
Edinburgh.

(with 2 figs. in the text)

CONTENTS

That part of the physiological life history of the tick, Ixodes ricinus, which is dealt with in the present paper falls into three separate and distinct phases, maturation of the gonads, oviposition and development of the egg; these three are collectively referred to as reproduction. It was felt desirable to deal with the development of the egg under this general heading rather than when dealing with the metamorphoses of the gorged larval and nymphal stages, partly since it may be argued that, strictly speaking, it must include the ontogeny of the new individual, before the term 'reproduction' is justified and, more particularly, because the development of the gorged tick and of the egg present two distinct problems. Thus, the development of the nymph or adult, from the engorgement of the preceding stage to the final moulting, may be regarded as one process; further, it follows on the engorgement phase, the conditions of which are subject to little or no microclimatic variation, although some degree of variation may possibly occur in the nature of the food supply. In the case of the egg, on the other hand, its developmental phase is merely a part of its history, the rest of which - the formation and deposition of the egg - may be subject to wide climatic variations, the possible effect of which variation in the subsequent developmental phase requires to be considered.

PRE-OVIPOSITION PERIOD

(a) Duration of pre-oviposition period at different temperatures and humidities

The influence of the different climatic factors on the development of the gonads of orthropods has received little attention. In the case of ticks, Cunliffe (1921) showed that the pre-oviposition period in Ornithodorus moubata averaged 29 days at 22°C and 15 days at 30°C. Similarly, Bishopp (1932) found this period to be longer, in the case of the cattle tick, at low than at high temperatures. Observations on the duration of the period at different seasons have been recorded by Hooker, Bishopp and Wood (1912) and Bishopp and Wood (1913) for many of the North American ticks. No data have been recorded of the effect of climate on this period in Ixodes ricinus. The existing information on the duration of the period may be summarized as follows:-

Authors	Temperature	Days
Wheler 1899	-	22
Samson 1909	-	14
Nuttall 1913	24°C	17-24
Olenev 1927	-	4-24
Elmanov 1930	-	6-14
Falke 1931	20°C	8-10
MacLeod 1932	15-21°C	14-52 (usually 15-22)

Newly gorged female ticks, in each case with a male attached, were subjected to different combinations of temperature and humidity as the ticks became available. Table I records the time elapsing/

TABLE I

Recording the Duration of the Pre-Oviposition Period at Different Temperatures and Humidities

R.H.	Temperature °C									
	2-3°	10°	14-16°	17-19°	20°	22.5°	25°	27.5°	30°	33-34°
100	No egg laying	33	15	20 16 13	16	12 10 17	22 9	32 25 16	+ +	+ +
			19	21 21 14	20	11 8	16 8	11 9	+ +	+ +
95			16			8	10 10			
90							20 11	24	+	
	+		15		16		11 10 9	11	+	+
85			24			16	10			
80		31	17		25		12 10 +		+	+
75			25 +		+ +		+			

+ indicates death without

- to face p 3

elapsing before oviposition began in each case.

At any particular combination of temperature and humidity, there is a very considerable variation in the duration of the pre-oviposition period. The apparent tendency for the period to be shorter at high temperatures than at low is rendered insignificant by this irregularity; all that can be safely inferred from the table is that at the extreme limits of temperature and humidity, i.e. at 27.5°C, 100 to 90 R.H; 20°C, 80 R.H., and 14.16°C, 75 R.H., the period is longer than at median temperatures and high humidities. In actual fact, at many of the extremes, particularly of humidity, oviposition was abortive, only some few dozen eggs being laid.

It is of interest that the shortest period obtained at any combination was 8 days, whereas two Russian workers, Olenev and Elmanov, record shorter periods.

(b) Lower limiting temperatures for maturation of ovaries

In Table I, "no egg-laying" is recorded for the combination 2-3°C, 100 R.H. This means that in the two-months' period during which the females were under observation, oviposition had not commenced. The experiments were then discontinued. It was apparent, however, that the method used involved a possible source of error; the absence of oviposition/

oviposition might not necessarily mean that the gonads were not mature; it might merely be due to the two processes having different critical temperatures. To test this, a gorged female which had been kept at room temperature, 15-18°C, for 7 days, was placed at 2°C and left for 6 days. It was then returned to room temperature, 100 R.H., and oviposition started 6 days later, i.e. 19 days after engorgement. Another female, immediately after engorgement, was placed at 2°C, 100 R.H., and left there for 3 months. Nine days after removal to room temperature, egg laying commenced. The experiment was repeated, two females being left for 3 months at 2.3°C. Oviposition began 10 days after removal to room temperature. It is probable, in view of the normal duration of the period at room temperature, that some degree of development of the ovaries took place at the lower temperature, i.e. that maturation may occur to some extent at temperatures as low as 2-3°C.

OVIPOSITION

(a) Limiting temperatures and humidities

A study of Table L indicates the limiting conditions of temperature and humidity for oviposition. A striking feature of the result is the comparatively low upper limit of temperature - between 27.5°C and 30°C. Again, as in the case of metamorphosis of/

of gorged ticks and also of survival of unfed ticks, the lower limiting humidity is high - 75 to 80 R.H. at temperatures of 14-25°C.

As has been stated above, no oviposition took place at 2-3°C over periods of 3 months. To determine whether this was due to the inhibitory effect of such a low temperature, or merely to the extremely slow rate of maturation of the eggs, the following experiment was made.

Three females which had commenced egg-laying at room temperature were placed at 2-3°C. Oviposition ceased and no eggs were laid during the next three months. The females were then returned to room temperature, and within a few days ovipsoition recommenced. It would appear, therefore, that whereas development of the ovaries may not be inhibited at this temperature, the actual process of oviposition is inhibited.

(b) Influence of temperature and humidity on course of oviposition

As in the case of the pre-oviposition period, no exact evidence is recorded of the effect of temperature or humidity on oviposition in this tick, or, indeed, little information of any kind with regard to the factors influencing the process. Nuttall (1913) records that oviposition lasted 32-45 days in May, and 44-45 days in April.

The/

TABLE II

Oviposition at Different Temperatures and Saturated Air

Temperature						Mean Total	Mean Time	Mean Daily Average
14-18°	Total Output	1069	2156	1376				
	Days	40	33	36		1534	36	44
	Daily Average	27	68	38				
22.5°	Total Output	2052	1789	2263	1890			
	Days	32	28	34	23	2000	29	69
	Daily Average	64	67	64	82			
25°	Total Output	1890	2400	1043	1289			
	Days	26	25	18	20	1656	22	73
	Daily Average	73	96	58	65			
27.5°	Total	832	2300					

- 6 from p 6

The following records refer to female ticks exposed to controlled conditions at different times, as opportunity arose. A greater number of results would have been desirable, but, nevertheless, the evidence available, limited as it is, is worth presenting because of the ~~uniform~~ uniform tendencies betrayed. Table II records the total number of eggs laid by females in saturated air, and at different temperatures, together with the time taken. As might be expected, there is a considerable variation in the total for any one temperature, since the amount and nature of the blood meal will naturally affect the total. It is apparent from the table that the average total is not significantly affected by temperature. This is in agreement with the results obtained by Hunter and Hooker (1907) for Margaropus annulatus. Cunliffe (1921), on the other hand, found that, in the case of Ornithodorus moubata, the egg total at 30°C was 50 per cent. higher than that at 22°C.

The average time taken for completion of oviposition is progressively less with increasing temperatures. Although the results, taken individually, are not significantly different from each other, the regular trend of the averages suggests that, in all probability, there is a correlation between time and temperature (compare Nuttall's finding, quoted above)/

TABLE III

Oviposition at Different Humidities and 25°C

Humidity						Mean Total	Mean Time	Mean Daily Average
100	Total Output	1890	2400	1043	1289			
	Days	26	25	18	20	1656	22	73
	Daily Average	73	96	58	65			
90	Total Output	813	1840	980				
	Days	15	21	19		1211	18	65
	Daily Average	54	88	52				
80	Total Output	1120	1310	727	948			
	Days	24	18	18	19	1026	19	53
	Daily Average	47	73	40	50			

above). The average number of eggs per day has been estimated in each case, and the means of the results (end column) show a progressive increase with higher temperatures, suggesting that the decrease in the time taken at higher temperatures is due to the accelerated rate of oviposition, and not to a decrease in the number of eggs laid.

Table III gives the egg totals, time taken and daily average at 25°C and relative humidities of 100, 90 and 80. Here also, the results, though not statistically significant, are suggestively uniform in the trend of their means, and might justifiably be interpreted as indicating that the progressive decrease in the daily average, with decreasing humidities, is due, not to a lengthening of the time taken for oviposition, since the time is more or less constant (column 2 of averages), but to a decrease of the total (column 1). In other words, a decrease of temperature slows down the rate of oviposition, whereas a decrease in humidity results in a reduction of the total number of eggs laid.

Fig. I illustrates the course of oviposition, A, at one humidity and two temperatures; B, at one temperature and two humidities. The curves are based on the actual daily figures for one female in each case. Daily counts were made for all the females; the curves were drawn in each case and are more or

less/

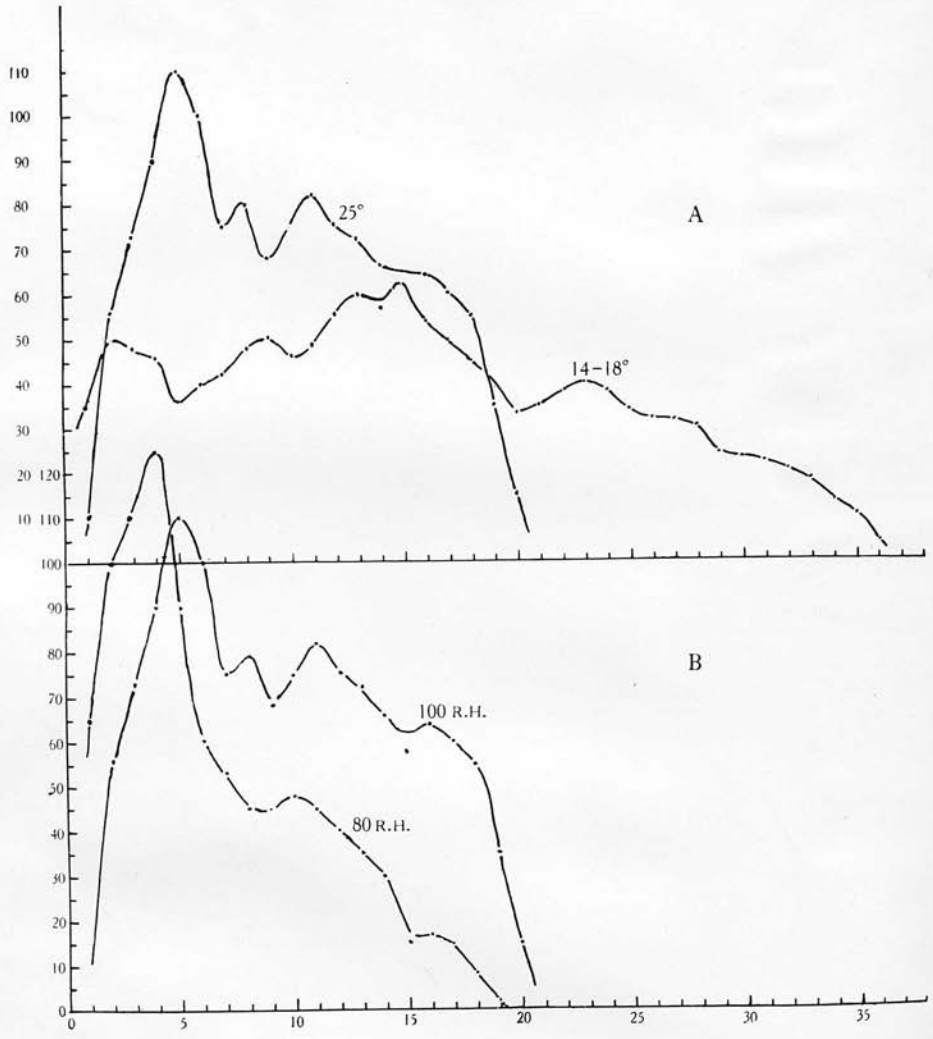

Fig. I The course of oviposition:

A at 100 R.H. and temperatures of 14-18° and 25°;

B at R.H. of 100 and 80 and temperature of 25°.

less similar to the types presented. These have been chosen merely because they approximated most closely to the average times and totals for their particular conditions. They represent, respectively, the following ovipositions:-

Conditions	Total	Days
14-18°C 100 R.H.	1376	36
25°C 100 R.H.	1289	20
25°C 80 R.H.	948	19

It will be seen that the oviposition curve betrays a uniform character, the daily deposition of eggs rapidly rising to its maximum, then falling away, more or less slowly, as the ovary becomes exhausted. Under favourable humidity conditions, the peak of the curve is higher, and is reached more rapidly at the higher temperature and exhaustion occurs after a shorter period. At the lower temperature, where metabolic activity is slower, the ovary takes longer to reach its maximum functioning rate, and maintains it over a longer period; the curves are, however, essentially similar. In the case of the female at the unfavourable humidity of 80 R.H., the result is different. At first, its oviposition curve agrees with that of the female at 100 R.H., but, within a few days, under the adverse moisture conditions, the ovary fails to maintain the daily output, which rapidly drops to a low value, and thereafter dwindles to/

to zero: oviposition ceases, not because the ovary has exhausted its potentiality for egg production, but because of the adverse external conditions.

DEVELOPMENT OF THE EGG

It would appear that the only controlled experiments on the effect of climate on the development of the egg of Ixodes ricinus are those of Olenev (1924, 1927). He states (1924) that, whereas under natural conditions eggs took 8 weeks to hatch, under artificial conditions at a temperature of 25-30°, they hatched in 3 weeks. They were killed by a humidity of 50-80 R.H. In a later paper (1927), he describes an experiment in which he placed eggs (1) on ice (0-17°), (2) in corridor (1-12°), (3) in forest (10-20°), (4) in tent (15-20°) and (5) in kitchen (25-30°). Hatching occurred after 300-400 days, 140 and 67 days, 61, 44 and 25 days respectively.

(a) Limits of temperature and humidity for development

It was hoped to obtain information both on the limiting conditions and on the percentage fertility of eggs under these conditions by subjecting batches of eggs of known number to the various combinations of temperature and humidity. Several such experiments were set up, and in all of them the same result was encountered - the eggs shrivelled, and no hatching/

TABLE IV

Recording the Time in Days taken for Development of Eggs

R.H.	Temperature °C							
	14-18	15-22	17-23	21-23	25-26	27.5	30	35
100	72	50	37	32	*24	*20	*18	+
	67	43	36	*30	23	16	+	+
	+		+	30	22	15	+	
	+		+	22	+			
				+	+			
					+			
90	+		37	28	27	19	19	
	+		37	25	25	18	+	
				+	24	17	+	
					+	+		
80			44	35	+	22	+	
			39	+	+	+	+	
			+				+	
75	+			+	+	+		
					+			

+ = death of egg

- 6 face p 10

hatching occurred except at one or two combinations, notably at 25°C and the higher humidities. It would seem that the manipulation of the eggs, incident on their enumeration, adversely affects their viability to a very marked extent, so that, even under favourable conditions, there is a tendency for them to shrivel. The expedient was then resorted to of using complete egg clusters; the results were recorded merely as "hatching" if any larvae appeared, or "death", no account being taken of the differential mortality rates. Table IV records the results of the various experiments. The values refer to the number of days between exposure of the egg cluster to the particular conditions and the hatching of the first larvae. A plus sign indicates that all the eggs died.

It will be seen that there is a wide variation in the times recorded, even for one combination of temperature and humidity. This is doubtless due to some extent to such variables as the age of the eggs, which varied from 0 to 10 days, and the temperature of the individual thermostats, which differed slightly for the different experiments, which were carried out over a period of two years. Four results are, however, strictly comparable; these are indicated by asterisks and will be referred to later.

It would appear that the lower limiting humidity for/

for development of the egg corresponds with that for development of the later stages, being in the neighbourhood of 80 per cent. saturation. The upper temperature limit for viability of eggs would appear to be slightly lower than that for the gorged larva and nymphs, apparently lying between 30° and 35°C.

(b) The threshold of development

It has been shown in a previous paper that the Thermal Constant theory cannot be used, in the case of the tick, as a basis for the estimation of the threshold of development. The approximate threshold might be determined by the method of plotting the velocity curve of development and producing it below the lowest point obtainable experimentally. This methos cannot be used here since sufficiently exact information of the development velocity of the egg at different temperatures is now available. It became necessary, therefore, to devise an alternative method. This consisted in exposing eggs to two temperatures sufficiently close to each other to obviate the possibility of their requiring, for completion of development, different amounts of heat - expressed in effective day-degrees or day-degrees over the threshold. The result allows of the probable threshold being obtained by calculation. It was felt desirable, in order that a true result might be obtained, to/

to reproduce, as far as possible, the conditions under which eggs would develop in nature, i.e. saturated air and a fluctuating temperature. Clusters of over two hundred eggs of the same age were used; the date of commencement of hatching in each case may reasonably be taken, therefore, as reflecting fairly accurately the true shortest time required for development under the particular conditions obtaining, since with such numbers individual variation is unlikely to upset the result. The egg clusters, which had not been counted or otherwise handled, were exposed in tubes over water in closed humidity systems. A temperature range exhibiting moderate fluctuations was obtained by the use of a water bath with a cold water circulation. The difficulty lay in reproducing these conditions with a slightly higher temperature, i.e. in obtaining a different temperature range, whose fluctuations should correspond in frequency and magnitude to those of the waterbath. An evaporation-cooled system was found to fulfil these requirements. A humidity system was wrapped in cloth, which was kept moist by a steady trickle of water. The rate of water flow in both systems was adjusted so that their temperatures differed by only a half-degree centigrade. Daily temperature records were then taken, and it was found that the temperature of the evaporation/

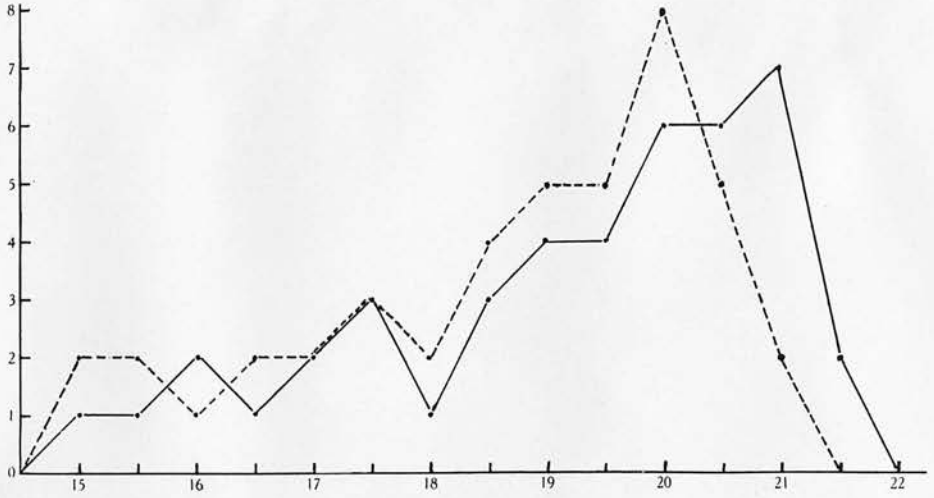

Fig. II The relation between the temperature of a water bath (whole line) and an evaporation cooled system (interrupted line). The curves show the frequency distribution of temperatures within their ranges of fluctuation.

evaporation system maintained a fairly consistent relation to that of the water bath. Fig. II shows the frequency distribution curves of temperature of the two systems from the commencement of the experiment until commencement of hatching in the water bath system. It will be seen that there was a close quantitative correlation between the fluctuations of the two systems, the evaporation system remaining approximately a half-degree cooler than the water bath.

The experiment was initiated on the same day as that on which eggs were laid. Hatching commenced in the water bath system on the 43rd day, in the evaporation-cooled system on the 50th day.

The mean temperature of the former over the 43 days was 19.2°C, that of the latter, over the 50 days, 18.7°C. Therefore, the total heat increment in day-degrees in each case was 19.2 x 43, or 826, and 18.7 x 50, or 935.

Let X = the threshold of development; then,

826 - 43 x = the number of effective day-degrees

= 935 - 50X (since it is assumed that the necessary number of effective day-degrees is the same for two temperatures so close together).

Therefore X = 15.5.

This result confirms that obtained in the case of/

of the gorged ticks, i.e. that the threshold of development lies in the neighbourhood of 15°C.

This conclusion is, of course, permissible only if it is assumed that hatching of the egg occurs immediately development of the contained larva is completed, and is not dependent on a particular set of extrinsic conditions occurring. This assumption seems reasonable, but there is no direct evidence on this point. Incidentally, it has been found that hatching of fully developed larvae would not occur at 2-3°C over a period of exposure of 48 days.

(c) Influence of oviposition conditions on development and fertility of eggs

It has been pointed out earlier that the development of the egg presents rather a different problem to that of the gorged larva or nymph, since its development represents but one phase, prior to the inception of which the egg, or, rather, the ovigerous female, is exposed to variable climatic vicissitudes. It is, therefore, necessary to consider the influence, if any, which such variations may have on the future history of the egg.

In the following experiment, the conditions considered were: low temperature with low humidity, low temperature with high humidity, high temperature with high humidity and high temperature with low humidity. The effect of each of these combinations of conditions during/

TABLE V

The Effect of Oviposition Conditions on the Subsequent History of the Eggs

Developmental Conditions	Time for Development in Days			
25° 80 R.H.	Died	Died	Died	Died
25° 100 R.H.	27, 29	23, 24	24, 24	28, 28
R.T. 100 R.H.	Killed by mould	36, 37	40, 40	38, 39
R.T. 80 R.H.	Died	39, 44	47, 48	Died
	R.T. 80 R.H.	R.T. 100 R.H.	25° 100 R.H.	25° 80 R.H.
	Oviposition Conditions			

R.T. = Room Temperature, which fluctuated from 17° to 23°, being mostly 20°C

— to face p 15.

during development was tested on eggs which had been laid under each of these combinations. Gorged females which had begun egg-laying were exposed to the appropriate conditions for one week. The egg clusters laid during this period were removed and exposed in duplicate to the various developmental conditions.

Table V summarizes the experiment, the results being set out so that each horizontal line refers to eggs exposed to a particular set of developmental conditions, the history of their disposition being different in each case, whilst each vertical column refers to eggs with identical histories as regards their disposition and with varying developmental histories. The results suggest the following conclusions:-

(1) The rate of development at a particular temperature is not greater in the case of eggs laid under conditions of high temperature than in the case of those laid under low temperature conditions, i.e. a high temperature during oviposition does not result in an accelerated rate of development of the egg.

(2) Under optimum conditions (25° 100 R.H.), the rate of development at one temperature is markedly affected by the humidity conditions/

conditions under which oviposition occurred: it is retarded when these were low, irrespective of what the temperature had been. This effect is not apparent under sub-optimal temperature conditions for development, i.e. room temperature (RT) 100 R.H. Under sub-optimal developmental conditions, both of temperature and humidity, there is a differential vitality exhibited by eggs laid under different humidity conditions, irrespective of the temperature at which they have been laid; that is, exposure of the female during oviposition to low humidities adversely affects the vitality of the eggs produced.

(d) Velocity of development of eggs at different temperatures

In the above experiment, the room temperature fluctuated between 17 and 23.5° C. Egg clusters laid at this temperature in saturated air and left to develop began hatching in 36 and 37 days. The general run of temperature over the 37 days may be gauged from the distribution:-

17°	17.5°	18°	18.5°	19°	19.5°	20°	20.5°
2	1	2	1	2	4	11	1

21°	21.5°	22°	22.5°	23°	23.5°
4	2	1	2	3	1

The mean temperature was 20.25°. That is, eggs at

20.25/

20.25° develop in 36 days. We have seen that at 19.2°C eggs developed in 43 days.

In Table IV, four comparable results are given. The eggs were of the same age, 0-4 days old, and were exposed at the same time. The results are 30, 24, 20 and 18 days for temperatures of 22.5°, 25°, 27.5° and 30° respectively.

If we assume the threshold of development to be 15.5°, the heat increment in terms of effective day-degrees necessary to effect completion of development at each of these different temperatures is as follows:-

Temperature	Days	Effective Day-Degrees
30°	18	261
27.5°	20	240
25°	24	228
22.5°	30	210
20.25°	36	170
19.2°	43	160

It is clear that the necessary increment of effective day-degrees - the 'thermal constant' - is not a constant value, but increases with higher temperatures; that is, the developmental value of a day-degree becomes less as the temperature rises. This is in agreement with the result obtained for the developing larva.

An interesting point in this connection is that at/

at the last two temperatures the necessary heat increment is markedly less, even relatively speaking, than at the other temperatures. These two temperatures represent the mean values of fluctuating temperatures. It is possible that fluctuating temperatures result in an acceleration of developmental velocity, as compared with stable temperatures amounting to the same total in terms of day-degrees. No evidence of such an acceleration, however, was obtained in the case of the development of gorged larvae at fluctuating as opposed to stable temperatures.

DISCUSSION

This paper forms the third of a series of laboratory studies on the relation of the tick, Ixodes ricinus, to its physical environment, the two factors chiefly considered being temperature and moisture. In the first two papers (1934, 1935) the author recorded the effects and intereffects of these factors on development of the gorged ticks and on general activity and survival of the unfed ticks. The present paper deals with the relation of climate to reproduction, including development of the egg.

Perhaps the most interesting feature of the results is the much greater significance of the humidity than of the temperature factor in the control of/

of reproduction. Apart from the adverse effects of extreme temperatures, near the limits of the range, this factor does not appear to exercise any profound effect on the physiological activities associated with reproduction. Thus, it does not appear to influence significantly the maturation of the ovary or its total output, nor does its impress during oviposition materially affect the subsequent history of the egg. The humidity factor, on the other hand, appears to be intimately related to the course and extent of certain of these processes. It would seem to control directly the total egg output of which the ovary is capable. Further, the humidity conditions obtaining at the time of oviposition influence strongly the subsequent fate of the egg, both as regards its viability and its rate of development.

In so far as the extent of the favourable ranges of these factors is concerned, the humidity requirements are similar to those for development, i.e. a restricted range of high moisture content. The temperature range, on the other hand, shows some interesting departures from the limits required for development. The results suggest that the metabolic activities of the period between completion of engorgement and initiation of oviposition can proceed, to a limited extent, at temperatures as low as 2-3 °C.

Oviposition/

Oviposition can proceed at temperatures well below the threshold of development, i.e. at 10°C, while the upper temperature limit for this process is distinctly lower than that for development, lying between 27.5° and 30°C. The limits for development of the egg approximate to those for development of the gorged stages. The threshold appears to lie about 15° - 16°C; the upper limit of temperature, however, is slightly lower than that determined for the gorged larva.

It is of interest that the temperature range favourable to reproduction should correspond more closely to the range favourable to general activity than to that for development. Different workers have recorded a similar finding in the case of insects. The possible significance of this in relation to the seasonal life cycle of the tick will be discussed in a later paper, in which it is intended to correlate the various laboratory findings with field observations on tick distribution and activity.

REFERENCES

Bishopp, F.C. (1932). Abst. Doctor's Dissertations, No. 9. Ohio St. Univ. Press, 1932.

Bishopp, F.C. and Wood, H.P. (1913). Parasit. 6, 153.

Cunliffe, N. (1921) Ibid. 13. 327.

Elmanov, N.V. (1930). Abst. Plant Protection. 7. 193.

Falke, H. (1931). Z. Morph. u. Ökol. Tiere. 21. 567.

Hooker, W.A., Bishopp, F.C. & Wood, H.P. (1912). Bull. U.S. Bur. Ent. No. 106.

Hunter, W.D. & Hooker, W.A. (1907). Ibid. No. 72.

MacLeod, J. (1932). Parasit. 24. 382.
- (1934). Ibid. 26. 282.
- (1935). Ibid. In press.

Nuttall, G.H.F. (1913). Ibid. 6. 91.

Olenev, N.O. (1924). Plant Protection. 1. 36.

Samson, K. (1909). Z. wiss. Zool. 93. 185.

Wheler, E.G. (1899). Proc. R. Agric. Soc. Eng. 4. 626.

IXODES RICINUS IN RELATION TO ITS PHYSICAL ENVIRONMENT

IV. An Analysis of the Ecological Complexes Controlling Distribution and Activities

by

JOHN MACLEOD

Carnegie Research Fellow,
Moredun Institute,
Edinburgh.

CONTENTS

I. Introduction

Numerous records exist of the occurrence, both regional and seasonal, of the tick, Ixodes ricinus. World distribution records have been collected by Nuttall (1911, 1916), Senevet and Rossi (1926) and Olenev (1929, 1934). In 1932, the writer recorded detailed observations on the seasonal and regional distribution of the tick in Scotland. In previous papers of the present series (MacLeod, 1934, 1935, 1935a), the relation of the tick to its physical environment has been dealt with in some detail, studies being made of the factor complexes governing survival, activity, reproduction and development. From the results obtained under laboratory conditions, it should now be possible to interpret, to some extent at least, the observed phenomena of seasonal and local distribution in terms of the underlying causes, and to outline the probable limits of world-distribution of the species.

It is well known that biological activities generally are intimately affected by meteorological factors, which, by their combined effects, impose the ultimate limits to the distribution and activities of most free living organisms. Imms (1931) defines the relationship as follows:-

> "Climate may be defined as the complex of meteorological factors prevailing throughout the year for a given area, while the incidence of these same factors at some particular point of time constitutes weather. Climate, in the broader/

broader sense, influences the geographical and ecological distribution of species, while weather influences their local prevalence by seasons: the one operates in space, the other in time."

With the tick, however, the position is complicated by the parasitic habit of life of the species; the evolutionary adaptations which usually accompany the habit might, therefore, be expected to modify the application of this general principle, and a survey of the biotic relationships of the tick becomes necessary.

II. The Influence of the Biotic Environment

On *prima facie* consideration, the local and geographical distribution of the tick would be expected to depend primarily on biotic factors, since, as a parasite, it is dependent on the presence of its host. Enemies, both predaceous and parasitic, might be expected to play an important part in controlling it, since it is exposed to their attacks both in its parasitic and in its free-living phases.

(a) Hosts and world distribution

A study of the rôle of alternative hosts (MacLeod, 1934a) showed that the presence of the chief host is not necessary to the continued existence of a tick population: even a restricted range of alternative hosts was able to maintain it at an appreciable level. When the possible alternative hosts/

hosts from which the tick has actually been recorded are considered, it is seen that the tick has a host list of extraordinary catholicity, ranging from sub-tropical lizards to the Arctic fox; embracing carnivores, from the polecat to the puma; herbivores of such widely differing geographical range as the red deer and the camel; rodents; and a wide range of birds, varying from predaceous falconids and owls to the sportsman's game-birds, and even to the unlikely cormorant. The geographical distribution of the species, therefore, is not likely to be intimately dependent on the host factor. Actually, the northern limits of occurrence, as judged from available records (vide infra), fall short of the limits of forest and agriculture; that is, the tick range does not extend to the limits of distribution of its possible hosts. It would appear, therefore, that physical rather than biotic factors govern the world distribution of the species.

(b) Enemies in relation to local and seasonal prevalence

The possibility remains that local distribution or seasonal prevalence in a climatically favourable area might be governed by biotic factors, such as the presence of a particular predator or parasite. The only known parasite of this species, however, is Hunterellus hookeri (Ixodiphagus caucurtei, du Buysson),/

Buysson), which has been recorded from Ixodes ricinus in France. Cooley and Kohls (1934) have studied the possibility of this parasite establishing itself in America, and have come to the conclusion that, in the Transition Life Zone, only one generation a year is possible, although conditions may be more favourable for multiplication in the Upper Austral Life Zone. If only one generation were possible in the year, the biology of the parasite, in outline, would be that the eggs would overwinter in parasitized ticks, develop in late spring and summer and emerge in autumn to parasitize the ticks then appearing. Even were two generations in the year possible, the degree of dispersal of this species of tick in nature is such that a sufficiently high percentage of parasitization is improbable, since the principal hosts, herbivores, do not tend to return, like carnivores, always to the same haunts.

There is no evidence of the effect of predators on the free-living tick population, though, doubtless, many fall victims to predaceous insects and birds. Field-mice also probably devour ticks, especially the large gorged females. During its parasitic phase, the tick is protected from the attacks of predators, with the possible exception of the starling, which, like its congener with the crocodile, whose/

whose teeth is picks, appears to have made a pact of mutual advantage with the sheep.

From the foregoing review, it would appear that the tick is singularly happy in its lot as regards its ecological niche; it does not suffer markedly either from individual or interspecific competition, and it occupies the fortunate position of a loose end in the food-chains of the animal community, being comparatively free from hyper-parasitism, and, because of the absence of any gregarious tendency in the non-parasitic phase, being non-susceptible to devastating attack from predators. The significant variables in its environment, unlike those of most predators, would, therefore, appear to be physical rather than biotic.

III. Seasonal Periodicity

It has been shown that there occur, in Scotland, two distinct periods of tick activity, one in spring, the other in autumn. Wheler (1899) and Brumpt (1922) record a similar periodicity in England (Alnwick Park) and in France.

Wheler (loc. cit.) suggested that the explanation of this phenomenon lay in the mildness of the climate, which allowed of the spring-fed ticks developing/

developing rapidly, and thus being able to engorge again in autumn of the same year. He instanced in support of his suggestion the Tyne district, where only a spring period of activity occurred. The farms there were at a fairly high altitude, and the area cold and windswept. In Skye, on the other hand, where the climate is much milder, a double attack occurred.

This explanation assumes that all the unfed ticks become engorged in spring, and does not take into account the fact that the spring period of activity comes to an end at approximately the same time (early June), irrespective of whether the ground is heavily or lightly stocked with sheep.

(a) Cyclical diapause theory of winter inactivity

Falke (1931) explained the winter cessation of activity as being due to the onset in autumn of a state of torpor from which the tick does not emerge until spring, irrespective of weather conditions. This theory was supported by Totze (1933). Such an attunement of causally unrelated happenings (Roubaud, 1922, et seq.) or dissociation of originally related happenings (Cousin, 1932; Dawson, 1931) is apparently possible: these workers have produced evidence suggestive of the existence in certain insects of a synchronisation of hereditary rhythm with/

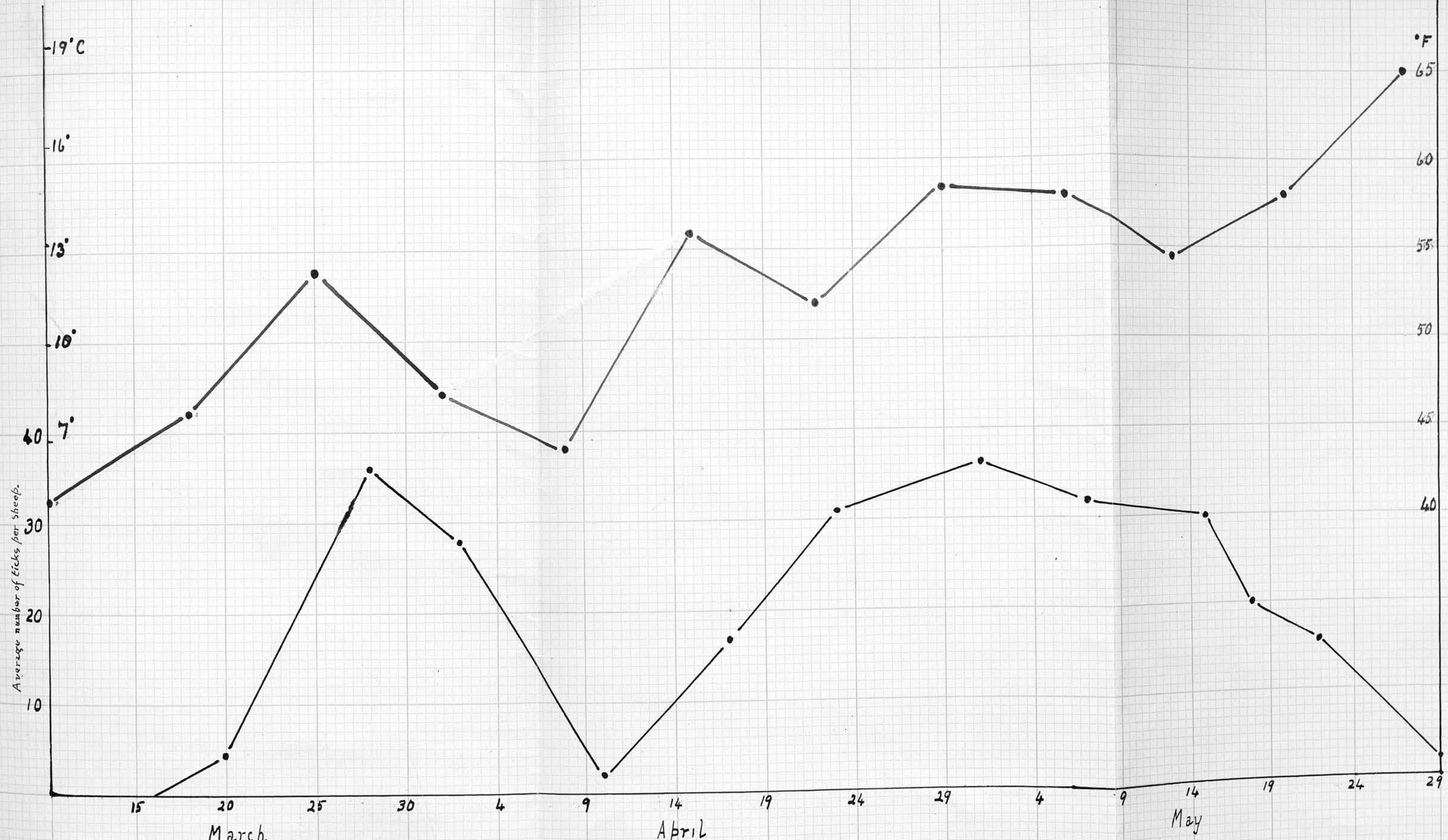
19°C
16°
13°
10°
7°
40
30
20
10
Average number of ticks per sheep.
°F
65
60
55
50
45
40
15
20
25
30
4
9
14
19
24
29
4
9
14
19
24
29
March
April
May
Weekly average of mean-maximum air-temperature.
Number of Ticks per sheep.

Fig. I.

correlation is illustrated in fig. 1, which shows the variation in tick infestation from the 14th March to the 29th May, 1934, for a farm in the Callander region. The weekly averages of the daily maximum temperatures for the nearest meteorological station (Perth) have been plotted on the same figure. Tick activity commenced when the temperature rose above 7°C and fell to a negligible level when it exceeded 16°C. In early April, there was a return to winter conditions, and the figure shows a corresponding drop in the degree of infestation for this period.

It does not necessarily follow from this correlation that air-temperature governs activity; proof of a causal relationship, however, is forthcoming from a study of the geotropic responses of the tick, for it has been shown (1935) that temperature determines the quality of the tick's response to gravity stimulus, the tick being negatively geotropic at temperatures of 14-24°C, while, above and below these limits, the response is positive. The apparent discrepancy between the observed and the experimentally determined limits is readily accounted for by the fact that air temperatures refer to the shade temperatures of the air, and are not comparable to the temperature of an object which is exposed to the radiant/

radiant heat of the sun. Thus, with a tick exposed on the tips of vegetation, an upper limit of 24°C would easily be reached by insolation when shade temperatures were in the neighbourhood of 15-16°C. Again, for the lower limit, it must be remembered that the elements of the microclimate in which the tick lives differ markedly from those of the macroclimate. Tutin (1928) has shown that the mean air temperature at Long Ashton during the greater part of the year is lower than the soil temperature at a depth of 4 inches, the difference sometimes being as great as 20°C. This difficulty of relating events in the lives of insects to climatic happenings, based on official meteorological data, is a serious one in most cases, since the majority of insects frequent specialized microclimatic types of habitat. The difficulty constitutes, in the writer's opinion, an outstanding objection to the use of bioclimatic ~~maps~~ charts, since the relationship between micro- and macroclimate will not be a constant one, but will vary both in time and space, and with edaphic factors in any given area.

Since the response of the tick to geotropic stimulus varies with temperature, it follows that temperature will determine the relative accessibility of parasite and host; a tick at the base of vegetation/

vegetation is obviously less likely to be picked up by a passing host than one on the tips. If the observed activity limits of 7° to 15-16°C be taken as the air temperature equivalents of the limits of negative geotropic response, it becomes possible to explain the seasonal nature of tick-activity as a temperature effect; at winter temperatures below 7°, the tick is at the roots of vegetation, at temperatures between 7° and 16°C, i.e. spring and autumn temperatures, it climbs to the tips of the vegetation and so becomes readily accessible to hosts, while, at temperatures over 16°C, summer temperatures, the tick, being again at the roots of vegetation, is less readily picked up. It has been shown, however (1935), that the temperature range for normal activity extends beyond the upper limit for negative geotropism; that is, at air temperatures over 16°, the tick may still be active. Thus, if a host should lie down on a tick, or, in browsing among grass roots, should come in contact with a tick, attachment could readily be effected. Thus it is that occasional ticks may be found on hosts throughout the summer months.

This "double attack" type of activity will be characteristic of countries with warm summers and cold winters, with fairly long transition periods between/

between these extremes. It follows that in colder countries, where the maximum summer temperatures do not exceed 16°C, there should be only one activity period, a summer one, while, in warmer lands, tick activity, if it occurred at all, should occur in winter only. A study of the available records of seasonal occurrence reveals that this appears to be the case. Thus, in central Russia, the ticks are found from May ("before the trees bud") to September (Olenev, 1927), while, in Algeria, they appear from November to April (Senevet and Rossi, 1924).

(c) Life cycle in nature

It has been shown in previous papers of this series that there are different temperature optima for activity, reproduction and development. The probable duration of the life cycle in nature must therefore be studied in relation to the seasonal occurrence of these optima; mere summation of the time required for completion of each stage is of only theoretical value. Various results have been obtained by the latter method. Falke (1931) gives 182 days, Elmanov (1930) 180-1874 days, Olenev (1927) 285-2194 days, Nuttall (1911) 178-2724 days: "about 170 days probably represents the shortest possible time required...", Stockman (1916) 160 days (spring eggs), 290 days (summer eggs), Wheler (1899) 33½ weeks./

weeks.

The following experimental data allow us to form some conception of the probable sequence of events in nature. The temperature range for parasitization is 14° to 24°C, whereas that for development is 15° to 35°C. Oviposition can proceed at temperatures of 10° to 27.5°C, and can commence in eight days after engorgement of the female. Development requires temperatures between 15° and 35°C. Translating these facts into terms of seasonal variations in Britain, one finds the tick functioning as a parasite under spring conditions of moderate temperature. High summer temperatures are unsuitable for active parasitization, which is consequently infrequent, but this season provides the optimum conditions for development of the ticks gorged in spring. Many of these are ready, therefore, to act as parasites again by the time suitable conditions are provided in the moderate temperatures of the autumn. The winter is passed either in the gorged state, or, where the ticks failed to parasitize a host during the short autumn season, in the unfed state. Those ticks which hibernated as unfed ticks appear at the beginning of the spring tick-season. The autumn-gorged ticks develop slowly during the late autumn and early spring months, whenever the temperature

of/

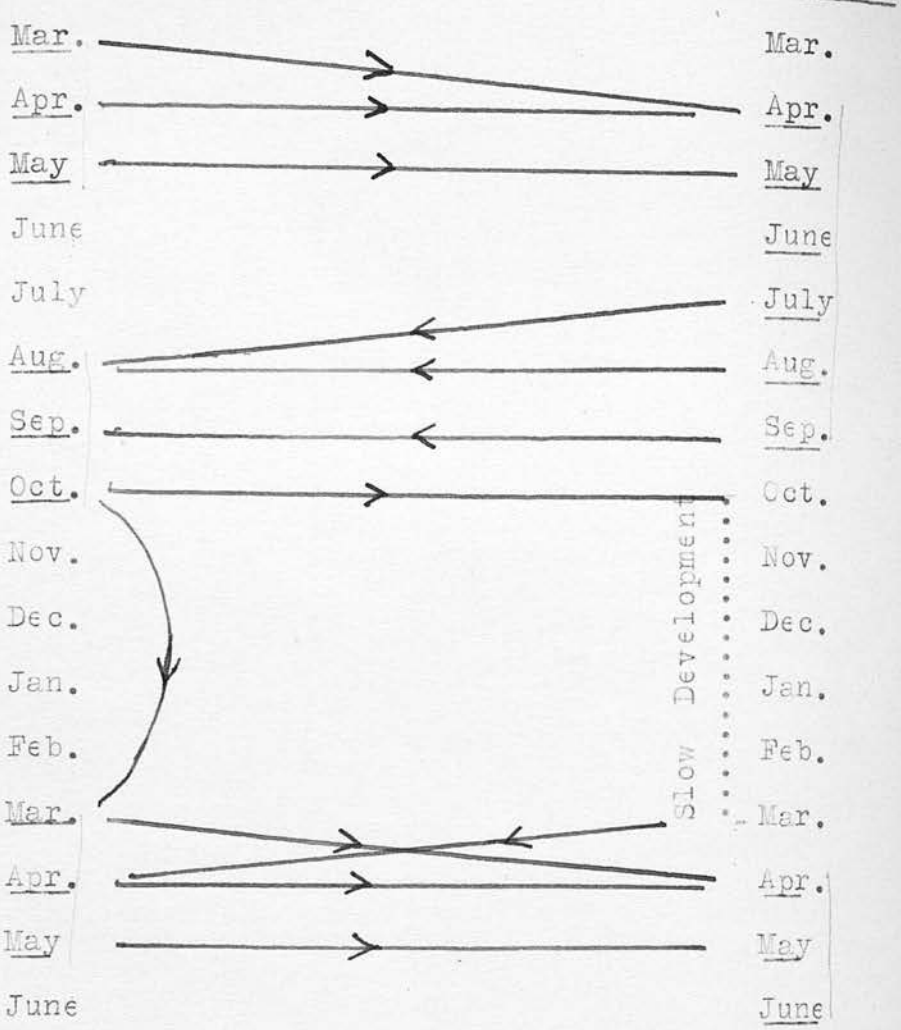

Fig. II - The relation between the seasons and the appearance of the unfed tick. Favourable months are underlined in their respective columns. Spring-fed ticks enter on development in April - May, and become ready to parasitize hosts from July - September. Parasitization is effected in August - October, or, failing that, in the following March. In April onwards appear those ticks which fed in autumn and developed during October - March.

- to face p 13

of the microclimate exceeds the developmental threshold of 15°C. Gorged larvae and nymphs can complete development in three months at a temperature only 5° above the threshold (MacLeod, 1934); during the five months' period, mid-October to mid-March, there are normally sufficient days over 15° to allow of development being well advanced by March. Under the increasing temperatures of March, development is completed, and the resulting unfed ticks enter a parasitization phase under the favourable conditions of spring (fig. 2).

Winter and summer may, therefore, be regarded as development seasons, spring and autumn as parasitization seasons. The alternation in the seasons is repeated in the life history of the tick, - unfed larva, developing nymph, unfed nymph, developing adult. An apparent difficulty arises in the fact that the active adult phase is followed by two successive passive phases, that of the gorged female and of the egg. It is to be remembered, however, that the temperature range for ovulation, 10° - 27.5°C, corresponds more closely to the range for activity than to that for development. Also, under favourable conditions, the pre-oviposition period may be as short as 8 days, and seldom exceeds 30 days. Therefore, adult females, engorging during a parasitization season, find/

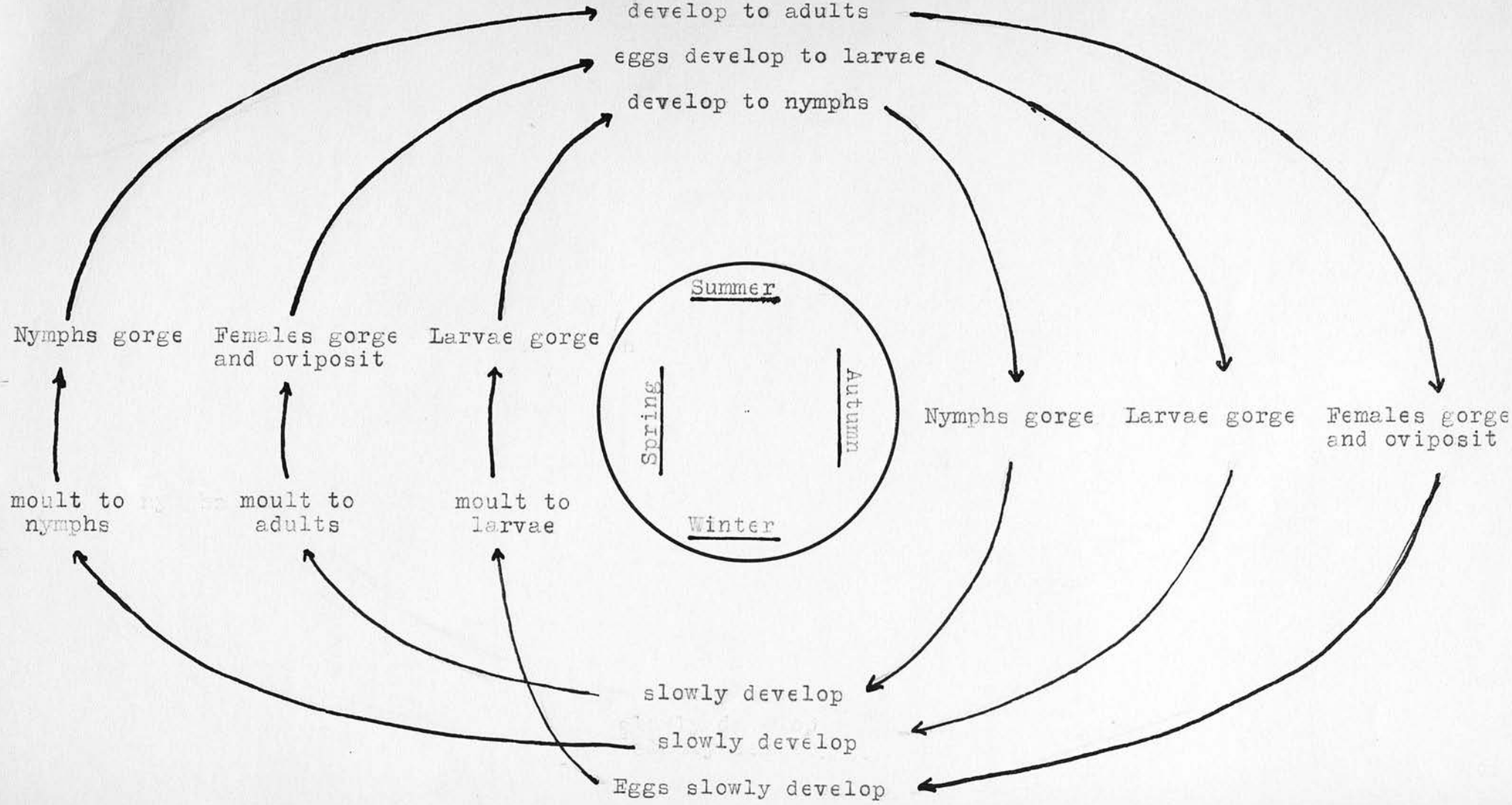

Fig. III.-- illustrating the seasonal life-cycle of the tick. The cycle is one and a half years, whether the generation starts with spring or autumn eggs.

find in that same season the conditions favourable to oviposition, and can generally complete the process before the seasonal limit is passed. The shortness of the autumn season is compensated for by the fact that oviposition can proceed at temperatures down to 10°C. Thus, the parasitization and oviposition phases of the female may be regarded as one phase, requiring moderate temperatures, and so the alternation of phases remains uninterrupted throughout the life history.

It would thus appear that, provided hosts are readily available, the life cycle takes a parasitization and a development season to each of the three stages, i.e. at least six seasons, or one and a half years, for completion. The cycle is illustrated in fig. 3.

Actually, there will be a wide variation in the time taken by different individuals to complete their cycle, according to the winter temperatures and to their success in finding suitable hosts. Since each unfed stage can survive at least a year, the duration of a particular cycle may be at least three years more than that outlined above, i.e. it may extend to four and a half years, or even longer.

IV. Habitat Requirements

The problem of the causes underlying the local distribution of the tick is simplified by the habit of feeding it has adopted. Being parasitic on its host, it can exercise no selection in relation to its habitat, and its physiological requirements, rather than any possible psychological reactions to habitat conditions, will determine its actual distribution.

Many observers record that the tick is most commonly found in swampy, undrained areas, or where a coarse vegetation of shrubs, bracken or heather is present. Olenev (1927), from a study of the moisture requirements of the tick, was able to show that this habitat choice was due to the high degree of humidity necessary for its survival and development. His conclusions have been confirmed by the writer, who showed (1935) that a relative humidity of over 75-80 is necessary for survival, reproduction and development at normal temperatures. Under conditions of arable pasture, such high humidity in the vegetation layer does not obtain throughout the year, the underlying soil frequently drying out for the top few inches during the summer. In swampy areas, however, where the water level of the soil remains

more/

more or less at the surface throughout the year, evaporation is never checked by water scarcity, and, providing there is a layer of vegetation to allow of a buffer stratum of still air remaining between the wet soil-surface and the outer atmosphere, a saturated, or almost saturated, microclimate is maintained even in summer. Thus, the factors which will determine the suitability of a habitat are primarily edaphic, the nature of the soil, the presence or absence of a humus-forming layer and the vegetation type. In Britain, the requirements are generally satisfied by hill sheep pastures: the soil is frequently peaty and, therefore, moisture holding; the vegetation is rank or coarse, and a mat is formed of the withered vegetation of the previous year. In such conditions, the tick finds its ideal home, sheltering, in winter and for reproduction and development, under the mat of decaying vegetation, climbing the stems of nardus, rushes, heather or bracken, to find its host.

(a) Comparison of different habitats

Measurements of the air humidity in different types of hill pasture were made in the spring of 1934, by means of a hair hygrometer. Three types were chosen: (1) old permanent pasture, with moss and tussocks of coarse grass - a common type of hill/

hill pasture; (2) ground inclined to be wet, but not strictly marshy - the vegetation layer consisting of old grass, rushes, etc; (3) marshy land, the vegetation type being chiefly rushes. The three areas were of small extent and intermingled; the actual dispersal of ticks over them may, therefore, be taken as fairly uniform.

The following were the humidity-readings for each type, and the corresponding air-humidity, as recorded by the same instrument:-

	Type 1	Type 2	Type 3	Air
April 18	70	100	100	60
24	87	95	100	56
May 2	89	99	100	65
12	78	98	100	58
18	75	78	97	60
29	87	84	96	62

The relative number of ticks on each type of habitat was roughly estimated by dragging a woollen blanket for a fixed distance (50 yards) over each type, and counting the number of nymphs adhering to the blanket. The results were as follows:-

Type	No. of Counts	Average Number of Ticks per Count
1	10	2.7
2	10	4
3	6	13

The result is open to objection since the counts/

counts were made over 2 or 3 days, and the number of ticks on the grass tips would vary with the air temperature; the evidence, such as it is, however, tends to support the general thesis of the dependence of population density on edaphic factors, where the host factor is constant.

It is clear that summer must be the critical time, in Britain, for tick survival, since at that season the humidity in the vegetation is most likely to decrease through drying of the soil. Many arable pastures afford sufficient cover and moisture for ticks in spring and autumn. Ticks introduced in autumn to such pastures by birds or brought in on hill sheep establish themselves as individuals, they moult, and may even engorge the following spring; yet, because of the summer drought, establishment as a species does not occur. Thus it is that, in spite of the frequent movement of sheep from hill to lowland pasture, the tick remains confined to the hill pastures (See MacLeod, 1932, for distribution in Scotland).

(b) Species spread in relation to ecological succession

If an arable pasture be allowed to deteriorate to such an extent that the soil becomes acid and moss begins to choke out the grasses, conditions become increasingly favourable for the tick. On such pastures,/

pastures, as the mortality from climatic causes decreases with changing vegetation type, dispersal is followed by individual establishment, and individual establishment gradually merges into the establishment of the species. Two actual instances of this sequence were brought to the writer's notice, where the ecological succession of vegetation-type in old permanent pasture allowed of ticks establishing themselves in lowland areas. In one case the farmer had been in the habit of renting his pasture as grazing for hill sheep in spring. Ticks were thus constantly being introduced, but previously had failed to survive, and fresh stock were put on these pastures in autumn with impunity. Latterly, however, the autumn-grazed herds suffered increasingly severe epidemics of tick-borne fever when introduced to this pasture. Examination of the sheep revealed the presence of engorging ticks; these had dropped from tick-borne fever carriers in the spring, had survived the summer, and were now spreading the infection to the non-immune lowland herd. Severe harrowing of the pasture to tear up the moss and heavy liming to lower the acidity were recommended as the obvious curative measures. The two instances afford good examples of the various phases in the spreading of a species, as defined by Elton (1927).

V. World Distribution

(a) Some general considerations

On the basis of results obtained in the laboratory, many attempts have been made to map, from meteorological data, the potential areas of distribution of different insects. The application of meteorological data in this manner is, however, on account of its misleading simplicity, full of pitfalls for the unwary, and a clear understanding of the underlying theory of climatology is necessary to a proper appreciation of the biological significance of any given set of data. One difficulty already mentioned is that of referring the macroclimatic values of a given area to specialised microclimates or even eccoclimates in that area. A further difficulty in the use of standard meteorological data is that these are given as means, and thus tend to obscure the extremes, although the latter intimately affect life, especially in the case of animals living near their geographical limits. With world isotherms, again, the temperatures employed for plotting these are, in the ordinary type of isothermal map, reduced to sea level; that is, they do not take into account the topography of the different areas. The actual temperatures along such isotherms/

isotherms may differ markedly from the given value, on account of varying altitude; therefore, from the biological point of view, such maps may be quite misleading.

It has been shown that the conditions necessary for survival of the tick are represented by a complex having its origin in the interaction of macroclimatic and edaphic factors. Since climate-type is not determined by any one factor alone, it is obviously impossible to define this complex in terms of one factor; the distribution of the tick must, therefore, be considered in relation to the climate as a whole, bearing in mind that, generally speaking, the vegetation type will be conditioned by climate.

In any given climatic type, distribution will be determined partly by the separate action of each factor, and partly by the interaction of the different constituent factors. Thus, rainfall is an important factor determining the humidity of the microclimate, but this will also depend, to some extent, on the rate of evaporation. Therefore, the velocity and direction of the prevailing wind must be considered, for the value of the wind as a desiccating agent will depend largely on whether it has travelled over land or sea areas. Again, the nature of the soil is important: a porous soil will absorb heavy

rain/

rain without leaving any moisture accessible at the surface, while a heavy soil will result in abundant microclimatic humidity with a much lesser amount of rain. The geological factor even will affect the value of rainfall, e.g. an impervious stratum will allow of marshy areas forming, as in the Roman Campagna, where the impervious volcanic floor has resulted in surface-water stagnating even under moderate conditions of rainfall.

Temperature also will have important intereffects with other physical factors. Soil-type will affect the response of the ground, and, therefore, of the microclimate, to temperature changes. High precipitation, where the temperature is below freezing, will ensure a snow-blanket, the biological significance of which is too well known to require statement. Sunshine will affect the ticks both directly by insolation and indirectly by radiation of heat from the ground; the amount of cloudiness will affect the value of insolation, a result of great significance at high altitudes, where, although shade-temperatures are greatly reduced below those at sea level, the ground-temperature under the rays of the sun may rise very considerably.

The various intereffects of this nature must be taken into consideration as well as the direct effects/

effects of separate factors, in discussing the suitability for the tick of different geographical areas for which meteorological data are available.

(b) Latitude and distribution

Senevet and Rossi (1926) summarized the existing evidence on the distribution of Ixodes ricinus and concluded that the species is a tick of cold or temperate climates. They found that, with a few exceptions, the areas from which the tick had been recorded were north of the 40 parallel of latitude. In a few instances, the tick occurred between this parallel and the tropics, and they suggested that in these regions development was inhibited by the heat and occurred only in winter, whereas, in temperate regions, it occurred in spring and autumn. The suggestion is due to an understandable misconception of the seasonal cycle of events; activity and development have been assumed to be synchronous. It has now been shown, however, that development occurs at temperatures above those necessary for activity, and can proceed at temperatures up to the limit for survival.

While latitude undoubtedly plays a part in determining the distribution of a species, any single parallel can seldom be expected to represent a limiting factor. The 40 parallel traverses the continental/

continental land-interiors and margins, and the climatologically unique Mediterranean basin; the land and sea distribution of the latter region has superimposed on the fundamental planetary régime along this latitude a complex variety of climatic types, which, collectively, differ from that found at the same latitude in the interiors and on the simpler marginal regions of the Pacific and West Atlantic. From the point of view of distribution, therefore, this parallel cannot be considered a bio-climatological unit.

Similarly, the northern limits of distribution are unlikely to be represented by a single parallel, since the north polar front is thrown into convolutions by the relief of the land masses in the northern hemisphere, bulging equator-wards in the lee of mountain ranges which impede the warmth-bearing westerly winds, e.g. east-wards of the Rockies and the Urals, and being forced polewards over the oceans. Olenev (1934) points out that the northern limiting zone for distribution of Ixodes ricinus lies generally between the 50 and 60 parallel, except between the 30 and 40 meridians, where the species has been recorded further north; he recognises, however, the importance of climate, among other factors, in determining the distribution of tick-species.

(c) Temperature requirements

Obviously, the two chief single factors affecting the tick are temperature and moisture. Since the moisture requirements are relative to the maximum moisture-holding capacity of the air and not absolute vapour pressure values, it follows that the conditions could be satisfied at almost any latitude. In contradistinction to moisture, temperature is largely governed by latitude and will, therefore, be the fundamental limiting factor to distribution. Within the geographical limits set by temperature, distribution will be governed by the climate-complex, the principal factor in which is rainfall, or, rather, precipitation in general.

The actual microclimatic temperatures critical for the tick, as determined by laboratory experiment, are as follows:-

Survival (1 day)	(-14° to -12°)	to 35°C
Parasitization	14°	to 24°C
Oviposition	10°	to 27.5°C
Development:		
Eggs	15°	to 30°C
Gorged Ticks	15°	to 35°C

It is clear, therefore, that, as regards temperature, survival of the species will depend on (1) the extremes in the microclimate not surpassing -14° and 36°, (2) the temperature remaining below 24-27° sufficiently long to allow of parasitization and/

and oviposition, and (3) the temperature remaining for a sufficiently long period at a value over 15° to allow of development.

As has already been pointed out, it is not possible in the present state of our knowledge to interpret at all accurately these limits in terms of air temperatures. The limits for parasitization in Britain were found to correspond to air temperatures of 7-16° (average weekly maxima). The mean monthly temperatures of the months during which this range occurred ranged from 5 to 10.5°C. It is by no means likely that these same air-temperature values would represent the same range in different countries. Bearing this objection in mind, however, an approximate index to microclimatic conditions can be obtained by using the mean-monthly isotherms. Thus, the isotherm of 10°C for the coldest month should represent, approximately, the equatorward limit of possible distribution, since at higher mean-monthly temperatures parasitization will not readily occur. Similarly, subject to a variable correction, which will often be of great magnitude, for soil-surface temperatures, the isotherm of 95 (mean maximum) for the hottest month will determine the extreme equatorward limit of survival. The correction factor, however, varies both in space and at different times in/

in the same area. Smith (1929) records observations at California over two successive periods of Feb. - Dec. and Dec. - June. Air-temperatures were compared with temperatures one-half inch below the soil surface; the ratio in the first period was 86 : 114, yet in the second only 81 : 76. On one particular date, when the air-temperature was 46-47°C, the temperature just below the soil-surface was 61-62°C.

As regards the poleward limits for survival, the difficulty arises that air temperature bears little relation to soil surface temperature when the ground is covered by snow. This dissociation is well illustrated by Mail's observations (1932): during one winter when there was an almost constant covering of snow, the air temperature ranged from -25°C to +8°C, yet, throughout the whole period, the minimum soil temperature did not go below -4°C. The effectiveness of freezing temperatures in limiting distribution will, therefore, be affected by the time of occurrence and the duration of the snow-coat, if this be present.

The poleward limit of distribution in relation to temperature will, however, also depend on the duration of soil temperatures over 15°. A very approximate idea of the relation between soil- and air-temperatures in cool-temperate regions can be obtained/

obtained in the following manner. It was found (MacLeod, 1932) that eggs exposed outside during the period May - July hatched in 9-10 weeks. The mean-monthly air temperatures for these three months in central Scotland range from 10 to 15°. Now, it has been shown (MacLeod, 1935a) that, under laboratory conditions, 9-10 weeks is the period taken for development of eggs at 14-18°.

A comparison of the time taken for development of eggs and of gorged ticks at several temperatures shows that the nymphs take about two and a half times as long to develop as the eggs thus:-

	17-23°	21-23°	25-26°
Eggs	5 weeks	30 days	24 days
Nymphs	13-24 weeks	78 days	61 days

Therefore, at 14-18°, nymphs would require over 20 weeks to develop; that is, 5 months with mean air-temperatures of 10-15°. Allowing a minimum period of 3 months with mean-temperatures over 10° for development in cool climates, that is, June, July and August in the northern, December, January and February in the southern hemisphere, the isotherm of 10° for June and December respectively can safely be regarded as including the furthest poleward limits of distribution of the tick.

Fig. 4 shows the tentative temperature-limits of/

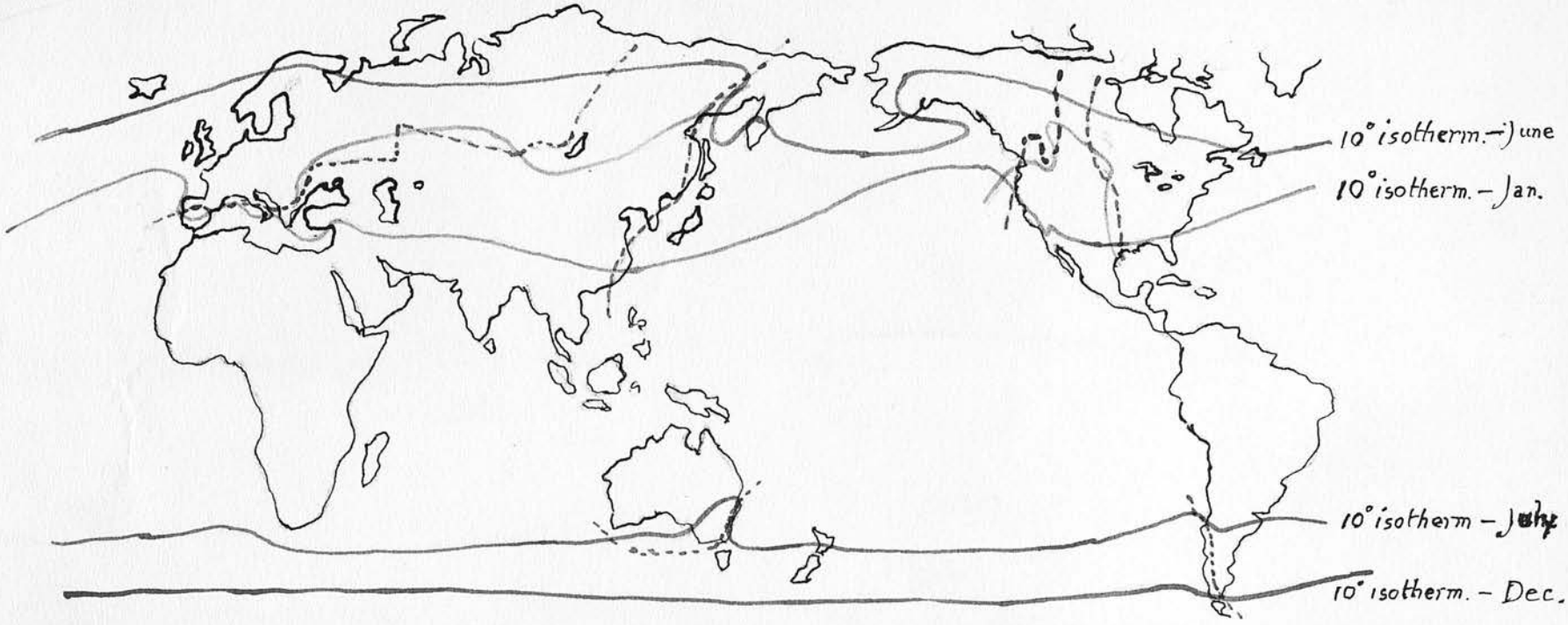
10° isotherm. – June
10° isotherm. – Jan.
10° isotherm – July
10° isotherm. – Dec.
hyetal equator
forest vegetation limits

Fig. IV.

of distribution so far defined. Olenev (1934) draws attention to the partial coincidence of the northern limits of distribution of tick species in general with the July isotherm of 15°. The agreement, however, is not complete, as this isotherm excludes Scotland and northern England, British Columbia and other regions where ticks occur.

(d) Precipitation requirements

The maintenance of high humidity in the microclimate depends on a number of factors other than rainfall: dew and mist may maintain almost saturated conditions, and yet have little appreciable effect on the recorded precipitation. Further, the actual rainfall will vary in effectiveness according to its nature and distribution. Thus, torrential downpours may result in a high rainfall value in a short period, yet much of this rain will often be lost by surface drainage.

It is improbable that rainfall can set an upper limit to distribution of the tick, since the species is extremely resistant to actual submersion (see MacLeod, 1935). Vorontzev (cited by Hooker, Bishopp and Wood, 1912) states that eggs of this tick can survive under water from Fall to Spring. With regard to the lower limit of rainfall, even were the distribution and nature uniform, the limiting amount would not/

not be a fixed value, but, to some extent, a function of temperature, since less is required to produce saturated conditions, and the rate of loss is less at low temperatures than at high. The rate of loss by transpiration will depend on the type of vegetation, forest transpiring more rapidly than grass. No precise meteorological limits, therefore, can be set to the areas favourable from the point of view of precipitation.

Generally speaking, climates with periodic rains, i.e. with regular dry seasons, should be unfavourable to the tick, as compared with climates experiencing rain at all seasons. On fig. 4, dotted lines have been drawn across the thermally possible areas of distribution, separating the two types of rain distribution.

The type of vegetation will play an important part in determining the effectiveness of rainfall by affecting the rate of evaporation back from the soil to the air. In turn, it is determined mainly by the distribution and amount of rain: forest requires a constant moisture supply, prairie grass is adapted to seasonal drought, while zerophilous desert plants clearly indicate more or less continuous drought. In the absence of detailed weather records, therefore, probably the truest index of the climate-type is/

is afforded by the major vegetation-type, provided due allowance be made for human interference, i.e. population-density, deforestation, irrigation, cultivation and so on.

The division between forest, including woodland, grass and cultivation on the one hand, and steppe, prairie, desert and tundra on the other, is indicated on fig. 4, and shows some degree of correspondence with the hyetal equator which divides areas receiving periodic rain from those receiving rain at all seasons. The climate-type indicated by forest and woodland is obviously that most suited, from the point of view of rainfall, to the tick, and in this connection it is of interest that Olenev (1931) describes a zonal distribution of different species of ticks in the U.S.S.R., Ixodes ricinus being principally confined to the forest zone of the northern regions. The prairie and steppe lands, stretching in a broad belt through central Eurasia and limited northwards by the hyetal equator, indicate a type of climate generally unsuited to the tick because of the parching droughts associated with this vegetation-type. Haviland (1926) describes the steppe as showing a surface of brown scorched grass in summer, "like a parched stubble field."

(e) Possible limits of distribution in northern hemisphere

The areas of possible distribution of the tick

have/

have now been roughly delimited from the point of view of the two main climatic factors, temperature and rainfall. The climate of the different regions within these limits may now be briefly reviewed, and the northern hemisphere will be first dealt with.

Generally speaking, western Europe, with the exception of the greater part of Spain, should be favourable to the tick, because of its typical marine climate, resulting in high rainfall, fairly evenly distributed, absence of seasonal extremes of temperature and a slow gradation of seasons, affording the moderate temperature-periods necessary for parasitization. The extreme temperatures and summer drought of central Spain place this region outwith the suitable limits.

Eastern Europe, in so far as it falls within the limits already set, remains comparatively favourable for survival of the tick, since except in the extreme east, the marine influence continues to be felt for long distances eastwards. The absence of high relief near the coast allows of the amount of orographic rain decreasing slowly eastwards, e.g. the 20 inch isohyet reaches to Moscow and Kiev. Similarly, the continental type of seasonal extremes in temperature has not established itself fully, except in the far east of Europe./

Europe.

East of the Urals, however, conditions are markedly different. Here several factors militate against survival of the tick. The continental type of climate is here strongly exemplified in the temperature-extremes. Siberia records the lowest temperatures in the world, yet the summers are extremely hot. The change from winter to summer and back to winter is not gradual, as in marine climates, but very rapid. The tick, therefore, is unable to effect parasitization and oviposition before the excessive heat of summer or the cold of winter inactivates it. A second reason why this region is unsuitable for the tick is the fact that under the influence of the winter high pressure centre here, precipitation is negligible - less than 1 inch for January. Snow will, therefore, be less heavy and its cover less constant than at the same latitudes elsewhere, and so the tick is not safeguarded from the killing temperatures of -50°F and even more which occur here in the winter months.

The effect of the fierce summer heat of this region will be intensified by insolation, since the skies are more cloudless here than at the same latitude further west. The mean annual cloudiness, although/

although largely determined by latitude, shows immediately east of the Urals and also in eastern Siberia, except on the coastal strip, a northern extension of clearer skies, while central Asia, from Asia Minor to Manchuria, has less than 50 per cent. of cloudiness.

The area east of Lake Baikal is outwith the limits set in fig. 4, until the eastern margin is approached. Here conditions are such that only a very narrow strip of the continental margin is suitable for the tick. The winter high pressure centre over Asia induces a continental type of climate with severe extremes and a rapid transition. This persists almost to the coast, as the constant monsoons prevent the influence of the sea making itself felt. Japan and parts of the coastline of Asia have a modified climate, the marine influence and the warm Pacific current inducing a temperature climate-type, with well distributed rainfall.

In western Canada and U.S.A., the mountain-ranges close to the coast limit the marine type of climate, corresponding to the European, to a narrow coastal strip. The arid area of the Rockies should, generally speaking, be unfavourable for tick survival, except where locally advantageous/

advantageous circumstances, such as local relief, vegetation-type and such, allow of favourable conditions occurring in limited areas. East of the 100 meridian roughly, the general type of climate is more suitable, from the point of view of rainfall. Continental type winter extremes of temperature occur, but their effect is to some extent obviated by the almost constant snow-cover. The eastern states are comparatively favourable, except for the peculiar superimposition of a continental climatic type on the marine, resulting in occasional severe heat-waves, during which lethal temperatures may be reached, and in irregular severe spells of drought.

Alaska, though coming to some extent within the limits set in fig. 4, is unlikely to favour survival of the tick because of the low temperatures prevailing over the peninsula, except for a narrow south-coastal strip. Further, the interior has a very low rainfall, only 10 inches annually in some places. Winter temperatures are extreme in comparison with those of north European regions of the same latitude, since the Pacific, blocked at the Behring Strait, cannot influence the Arctic limit in Alaskan reginns in the same manner in which the Atlantic, which has free access to the Polar Sea, affects the northern European/

European regions. In comparison with the positive winter temperature-anomaly of 20 to 30 in north-west Europe, Alaska has a winter anomaly of -2 in the interior to 10 on the south-west coast. The low precipitation prevents a snow-coat modifying the temperature-extremes at all effectively, and the winter low temperatures therefore should make the Alaskan region unsuitable for tick survival.

The potential areas of distribution of the tick in the northern hemisphere have now been delimited in a general way. It is to be remembered, however, that the different regions have been grouped according to their general climatic facies; the limits outlines must be regarded as defining, in a broad sense, the major regions of distribution. The possibility remains that within an unfavourable major region there may occur limited areas where meteorological and topographic factors combine to upset the normal climatic type, and result in isolated potential loci of tick-survival. Three regions in especial where the defined limits must be accepted with reserve are the Mediterranean basin, the land and sea distribution in which makes it impossible to classify the climate under one type, the central Asian plateau country, and the western American/

American plateau. In the last two regions, the complexity of relief, high altitude and topographically determined diversity of vegetation-type may readily result in comparatively favourable conditions occurring over limited areas.

Mountain areas on the equatorward side of the distribution limits present rather a complicated problem. Air temperatures are reduced, roughly 1 degree fahrenheit for every 300 feet of altitude, but, above a certain level, rainfall also is reduced. There will therefore be a tendency to aridity, which will be intensified by the clearness of the air and other factors inducing an acceleration in evaporation rate. The nature of the rainfall also tends to be tropical in its periodicity, and the rain usually falls in heavy showers, thus losing much of its effectiveness. Up to a certain height, on the other hand, precipitation tends to increase with altitude, resulting in forest zones. Where these alpine forests occur, they will exercise a marked effect on the microclimate. The summer soil temperatures will be lowered and the extremes modified. Transpiration also will tend to reduce the temperatures in the eccoclimate, and therefore in the microclimate, of the soil surface. It follows that no hard and fast rule can be laid down as

to/

to the suitability or otherwise of tropical and sub-tropical mountain regions. Generally speaking, however, it may be said that alpine forest zones in such latitudes indicate conditions possible for tick survival.

(f) Possible limits of distribution in the southern hemisphere

In the southern hemisphere, the only land areas falling within the specified limits are New Zealand, except for the extreme north, the south-east corner of Australia, Tasmania, the south of the Argentine and south Chile. Generally speaking, the New Zealand and Tasmanian climate is comparable to the English, except for Auckland, the summers being cool and the winters mild. The rainfall in South Island especially is evenly distributed, and there is nowhere a real summer drought. The rainfall in New South Wales, unlike that in most of Australia, is evenly distributed throughout the year, and the actual amount is fairly large. The annual range of temperature is comparatively limited, but sufficient to include parasitization- and development-conditions; this area, therefore, should be comparatively suitable for the tick.

Patagonia and Chile represent two extremes of climatic types. South Chile, on its western mountainous strip of coastline, receives the moisture/

Fig. V.

moisture of the west winds and has therefore a very high rainfall throughout the year. Its vegetation type is dense forest and swamp. The result of this, however, is that eastwards, across Patagonia and right to the coast, conditions are arid desert for most of the year. Only on the western seaboard, therefore, should conditions be suitable for the tick.

(g) Known distribution

The major regions outlined in the previous sections as being theoretically suitable for tick-survival have been shaded in on a world map (fig. 5), and on the same map the various areas from which the tick has actually been recorded are indicated by dots. The American records (listed by Nuttall, 1911, 1916) plus one in Florida (Giltner, 1927) must be treated with reserve, as possibly including varieties and sub-species of Ixodes ricinus. The single record of this species from Panama (Dunn, 1923) is surprising, in view of the definite thermal limits to its survival and activity. In the Old World, two tropical records occur, one in Eritrea (Franchini, 1927) and one in Hué (listed by Senevet and Rossi, 1926). These three records are inexplicable, and may possibly be due to faulty identification. The remaining Old World records fall within the specified limits/

limits, except for a few interesting exceptions. The Mediterranean basin has already been mentioned as a doubtful area, the climatic conditions of which do not fall readily into any simple classification.

The Armenian records (Yakimoff et al., 1934, Lototzkii and Popov, 1934) are extremely interesting, in that they occur in a limited area of definitely favourable conditions. The west winds, although parched by the European continent, renew their moisture over the Black Sea, and the Caucasus Mountains bordering it to the east thus receive a liberal supply of rain. The vegetation type consequently is dense forest. The second of these records is from a reginn at over 6,500 feet.

Two records exist of occurrence of the species on the high plateau in the Pamir region, one in Chitral (Sachs, 1934) and one in Kashmir (Nuttall, 1916). The possibility of this mountainous district including favourable areas of limited extent has already been remarked on, since the region is outwith the limits only on account of rainfall scarcity, the temperature requirements being satisfied. Locally advantageous conditions may also explain the Lake Baikal record, since the inhibiting factors in the Siberian region are considered to be absence of a protecting snow-cover and absence/

absence of transition periods between the temperature extremes. Irkutsk, however, records 65 days with snowfall in the year, and, further, the extremes in this area will be moderated appreciably, it being a general rule that lakes moderate the climate in their immediate vicinity to an extent roughly proportional to the size of the body of water (Miller, 1931).

In the southern hemisphere, the only existing record of Ixodes ricinus is that of a single specimen in New Zealand (listed by Senevet and Rossi, 1926).

Complete absence of the species from the antipodean favourable region would not have been surprising. Dispersal by ordinary means could hardly effect introduction, since the longest period the tick remains attached to a host is a matter of two weeks, and the tick would require to traverse the tropical and equatorial unfavourable belt to reach there by mechanical carriage in the active, unfed state.

The single record is, therefore, all the more surprising, since the suitability of the climate would indicate a high population density if the tick were at all present.

The difficulty of surviving the magratory passage from the northern hemisphere readily accounts also/

also for the apparent absence of the tick from the limited favourable area on the western seaboard of Chile, unless, as seems improbable, it were already established in southern America before the establishment of the present climatic belts.

VI. Philosophical Epilogue

The outstanding impression which is left by the foregoing ecological study is the strong impress of climatic as opposed to biotic factors on the periodicity and extent of the activities of this species. In this respect it fulfils the qualifications of non-parasitic organisms. Further, the parasitic habit occupies some three weeks altogether out of a life of one and a half to four and a half years, and, most important of all, does not cover the physiological phase which would most benefit from the protection of a sheltered life, namely, reproduction. It is hardly fair to stigmatise its complete dependence on other animals for food as a parasitic character, for, after all, it is no more dependent in this respect that many blood-sucking flies, and how do carnivores evade this criterion? In its rapacious levying of toll from its prey during intensive predatory periods, which it alternates with long periods of independent existence, it resembles the robber outlaw more than/

the blackmailer, the flea rather than the louse. Only in its inability to govern psychologically its reaction to other animals or to break facultatively the strict sequence of its life activities is it a parasite. By this "passivity of constitution," to use the term coined by Thomson and Geddes (1931) in their discussion of parasitism, is it damned, but the impression remains that its debasement is comparatively slight, and merits a rank in the category of degeneracy somewhat higher than that of obligatory parasitism.

An interesting speculation is that of the nature of the mechanism regulating tick numbers in nature. The potential increase of ixodid ticks generally is enormous: Lounsbury (1899) estimated 20,000 as the maximum number of eggs deposited by a female Amblyomma hebraeum, and the average deposition of 18 species, based on the records of 151 individuals given by Hooker, Bishopp and Wood (1912) was 3,120 eggs per tick.

The average deposition of this species under optimum condition (MacLeod, 1935a) is about 2,000 eggs. Since the ratio of females is 9 : 5, (MacLeod, 1932), it follows that in a stable population $1 - 9/5 \times \frac{1}{2,000}$ or 99.9991% of each generation succumb to the vicissitudes of their environment.

The/

The normal regulating mechanisms of animal numbers,— upsets of the balance of food chains, in which a species is involved, intra-specific competition, checking, either facultative or obligatory, of reproduction, and so on,—is unlikely to play any important part here, under normal conditions. The dispersal of the tick during reproduction prevents the likelihood of density producing psychological or other checks on reproduction, competition is practically absent because of the numbers and size of the available hosts, and the tick while on the host is comparatively immune from attack. The only likely biotic controls are predation during the free phase, and failure to effect parasitization.

Apart from these, the eliminating factors will be physical - desiccation, drowning, thermal extremes, accident of mechanical injury, and so on. These are uninfluenced by fluctuation of population numbers, and are not therefore automatic checks. The nature of the factor or factors maintaining equilibrium remains obscure.

REFERENCES

Brumpt, E. (1922). Précis de Parasitologie. 3rd Ed. Masson et Cie. Paris.

Cooley, R.A. & Kohls, G.M. (1934) Fifth Pacific Science Congress. Rep. B.5, p. 3375.

Cousin, G. (1932) Bull. Biol. Fr. et Belg. 15. Suppl.

Dawson, R.W. (1931) J. Exp. Zool. 59. 87.

Dunn, L.H. (1923) Amer. J. Trop. Med. 3. 91.

Elmanov, N.V. (1930) Abst. Plant Protection. 7. 193.

Elton, C. (1927) Animal Ecology. Sidgwick & Jackson, London.

Falke, H. (1931) Z. Morph. u. oekol. Tiere. 21. 567.

Franchini, G. (1927) Abst. Rev. App. Ent. B. 17. 144.

Giltner, L.T. (1927) J. Amer. Vet. Med. Ass. 72. 919.

Haviland, M.D. (1926) Forest, Steppe and Tundra. Cambridge.

Hooker, W.A., Bishopp, F.C. & Wood, H.P. (1912) Bull. U. S. Bur. Ent. No. 106.

Imms, A.D. (1931) Recent Advances in Entomology. J. & A. Churchill, London.

Lototzkii, B.V. & Popov, V.V. (1934) Abst. Rev. App. Ent. B. 23. 2.

Lounsbury, C.P. (1899) Agr. J. Cape of Good Hope. 15. 728.

MacLeod, J. (1932) Parasit. 24. 382.
(1934) Ibid. 26. 282.
(1934a) Anim. Ecol. 3. 161.
(1935) Parasit. 27. 123.
(1935a) Ibid. In press.

Mail/

Mail, G.A. (1932) J. Econ. Ent. 25. 1049.

Miller, A.A. (1931) Climatology. Methuen & Co. London.

Nuttall, G.H.F. (1911) "Ticks." Pt. 2. 296.
(1916) Parasit. 8. 294.

Olenev, N.O. (1927) Défense des Plantes. 4. 354.
(1929) C.R. Acad. Sci. U.R.S.S. 21. 489.
(1931) Z. f. Parasit. 4. 126.
(1934) Bull. Acad. Sci. U.R.S.S. 387.

Roubaud, E. (1922) C.R. Acad. Sci. Paris. 174. 964.

Sacks, A. (1934) J. R. Army Med. Cps. 63. 217.

Senevet, G. & Rossi, P. (1924) Arch. Inst. Past. Algeria. 2. 223.
(1926) Bull. Soc. Path. Exot. 19. 558.

Smith, A. (1929) Hilgardia. 4. No. 3.

Stockman, S. (1916) J. Comp. Path. & Ther. 29. 264.

Thomson, J.A. & Geddes, P. (1931) Life: Outlines of General Biology. Williams & Norgate Ltd., London.

Totze, R. (1933) Z. vergl. Physiol. 19. 110.

Tutin, F. (1928) Rep. Agric. Met. Conf. London, 1928. 57.

Wheler, E.G. (1899) Proc. Roy. Agric. Soc. Eng. 4. 626.

Wigglesworth, V.B. (1934) Insect Physiology. Methuen & Co. Ltd., London.

Yakimoff, W.L., Gousseff, W.F., Nezmetaieff, N.W. & Rastégaieff, E. (1934) Ann. Soc. belge Med. trop. 14. 235.